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# The Journal of ARACHNOLOGY

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## 16th International Congress of Arachnology



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# THE JOURNAL OF ARACHNOLOGY

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## HORIZONTAL AND VERTICAL DISTRIBUTION OF SPIDERS (ARANEAE) IN SUNFLOWERS

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**ABSTRACT.** Sunflowers are an increasingly important crop plant in the Czech Republic. The spider fauna of this crop has not been investigated yet. The aim of this study was to monitor the spider fauna of sunflowers and to study the seasonal change in the spatial and vertical distribution of this fauna. For this purpose a small experimental area was used where spiders on each single leaf of 50 sunflower plants were visually checked at monthly intervals from spring until autumn. The density of spiders increased during the season reaching a maximum of seven spiders/plant in the autumn shortly before harvest. The spatial distribution changed accordingly, being random in spring and early summer and normal or aggregated toward late summer. Two spider species, *Neottiura bimaculata* and *Theridion impressum* (Theridiidae), dominated (96% of all individuals) throughout the season. These two species exhibited a different microhabitat preference: *N. bimaculata* individuals were found particularly on the lower sunflower leaves, *T. impressum* preferred higher leaves. The density of the spiders (per leaf) was independent of the density of two dominant pest species, aphids and leafhoppers.

**Keywords:** Aphids, spatial distribution, agrobiocenosis, stratification, colonization

Although sunflowers are considered the second most important oilseed crop in the world (Cobia & Zimmer 1978), in the Czech Republic their importance was not recognized until recently when the current production had not been able to cover the need of our food industry (Jirátko et al. 1996). Since then the planted area has enlarged mainly in the south-eastern part of the country where the warmer climate provides suitable conditions for a high production.

In its native region, i.e. North America, the sunflower has many pests (Charlet & Brewer 1998). Thus it thrives better in foreign countries because it has left a multitude of pests and diseases behind. This is particularly true for Europe. In the Czech Republic the sunflower plants are attacked by only a few pests: aphids, leafhoppers, moths and heteropterans (Jirátko et al. 1996).

The fauna of natural enemies of sunflower pests has been so far investigated only outside Europe. It was found to be composed of various heteropterans, lacewings, coccinellids, ants and parasitoids (Lynch & Garner 1980; Boica Junior et al. 1984; Men & Thakre 1998). Spiders were also among the most abundant and important predators (Seiler et al. 1987; Royer & Walgenbach 1991). For example, an araneid species, *Neoscona nautica*

(L. Koch 1875), was found to prey on aphids and other pests on sunflower (Singla 1999).

As the fauna of predators occurring on sunflowers has not been investigated in Europe, the first aim of this study was to monitor spiders, particularly the change in their temporal and spatial distribution in a sunflower plot. Another aim was to observe the vertical distribution of the most abundant species of spiders on sunflowers. Very little attention has been paid to the stratification of spider fauna in agroecosystems (exceptions are He et al. 1995; Hao et al. 2000), obviously due to the intensive effort required for such investigation (Holland et al. 2004).

### METHODS

The study was performed in Praha-Ruzyně, the Czech Republic (50°06'N, 14°15'E, faunistic grid no. 5951). The sunflowers were planted in April 2003 in rows 80 cm apart, at a distance of 30 cm from one seedling to another. The total area was about 2,000 m<sup>2</sup>. In the middle of this area, an experimental plot (4 m × 7 m) including 50 plants was selected. The position (coordinates relative to the left lower corner of the plot) of each plant within the experimental plot was mapped.

The investigation began in late May when sunflower plants were 10 cm tall and termi-

Table 1.—List of spiders recorded species on the sunflowers during one season. Numbers are total records and the percentage from the total number.

Family/species	Number	%
Araneidae		
<i>Aculepeira ceropegia</i> (Walckenaer 1802)	11	0.70
<i>Araneus</i> sp.	1	0.06
<i>Araniella</i> sp.	4	0.20
<i>Mangora acalypha</i> (Walckenaer 1802)	1	0.06
Theridiidae		
<i>Enoplognatha</i> sp.	19	1.20
<i>Neottiura bimaculata</i> (Linnaeus 1767)	282	17.10
<i>Theridion impressum</i> L. Koch 1881	1301	79.20
<i>Theridion varians</i> Hahn 1833	2	0.11
Linyphiidae		
<i>Microlinyphia pusilla</i> (Sundevall 1830)	15	0.90
Thomisidae		
<i>Xysticus</i> sp.	6	0.40
Dictynidae		
<i>Dictyna</i> sp.	1	0.06
Total	1643	

nated in September shortly before harvest. Plants in the selected plot were examined at monthly intervals, i.e. altogether five times during the season. On each examination date every single leaf (upper and lower surface) of each of 50 plants was visually inspected to record the number of spiders present. The leaves were gently inspected not to disturb present spiders. The height of each plant was recorded on each date too. The spiders were not sampled, only visually inspected in order to record their change during the seasons. Further, on each date 25 plants were selected outside the experimental plot. On each plant one leaf was sampled in order to examine the number of spiders, aphids (unidentified), leafhoppers (unidentified) and other insects. All spiders were identified to species, if possible, or to a genus. Juvenile theridiid spiders were identified using Pekár (1999).

Statistical analyses were performed using STATISTICA (StatSoft). Distribution of spiders at each observation date was tested using Kolmogorov-Smirnov test (KST) for normality. Linear regression models (LM) were used to study the relationship between density and the season and the relationship between prey and spider densities. Since the data did not follow a normal distribution, log-transformation was used prior to analysis. Horizontal dis-

tribution of spiders in the study plot was studied using graphical spatial analysis. The analysis projects a three-dimensional dataset that includes two-dimensional coordinates of each plant and the spider density for each plant on a two-dimensional plane. The gradient of density is displayed as shades of gray with white color standing from 0 and black standing for the maximum density. The contours of density were modelled using distance weighted least-square method. Numbers represent means  $\pm$  standard error throughout the text.

RESULTS

**Horizontal distribution.**—More than 1600 individual spiders were observed during the study (Table 1). The majority of spiders (99%) were represented by theridiids. Two spider species, *T. impressum* L. Koch 1881 and *Neottiura bimaculata* (Linnaeus 1767) (both Theridiidae), accounted for 98% of all spiders, with the former species making up 79% of the spider fauna. The density of spiders on sunflowers increased over the study season. On 28 May 2003, there were  $0.27 \pm 0.09$  spiders per plant. On 25 June, the density increased to  $1.49 \pm 0.26$  and on 23 July it was  $1.12 \pm 0.20$  individuals/plant. On 20 August, the density further increased to  $6.78 \pm 0.68$  and on



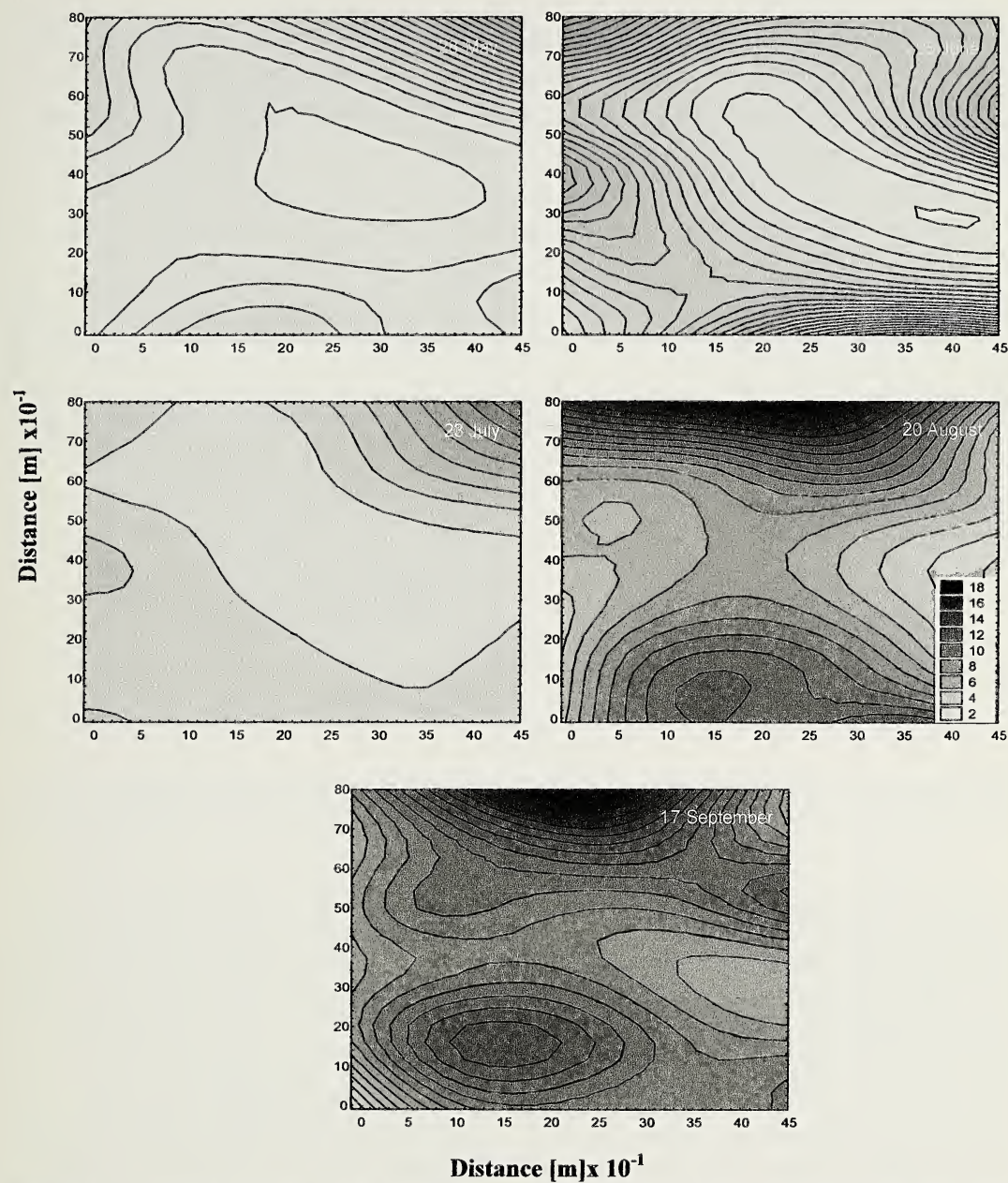


Figure 1.—Seasonal change in the spatial distribution of spiders on the sunflower plot. The graph represents the study plot. The shades of gray identify spider density (per plant) on individual plants: the darker the shade the higher number of individuals. Contours of densities were modelled using least-square method. Data from 50 plants in one 4 m × 7 m plot, inspected repeatedly.

17 September it was  $6.98 \pm 0.76$  spiders per plant. The overall density thus increased following a linear model  $y = -0.48 + 0.07 \times x$  (LM,  $R^2 = 0.91$ ,  $P < 0.04$ ). The average increment was thus 3.5 spiders/plot/day.

Although the mean spider density of the entire plot increased during the season, detailed

analysis of each individual plant revealed that there was a change of density within the plot. The highest increase (5.7 times on average) in the density was recorded from July–August, i.e. in the period following breeding when spider density increased on 88% of the plants. A less pronounced increase was found from



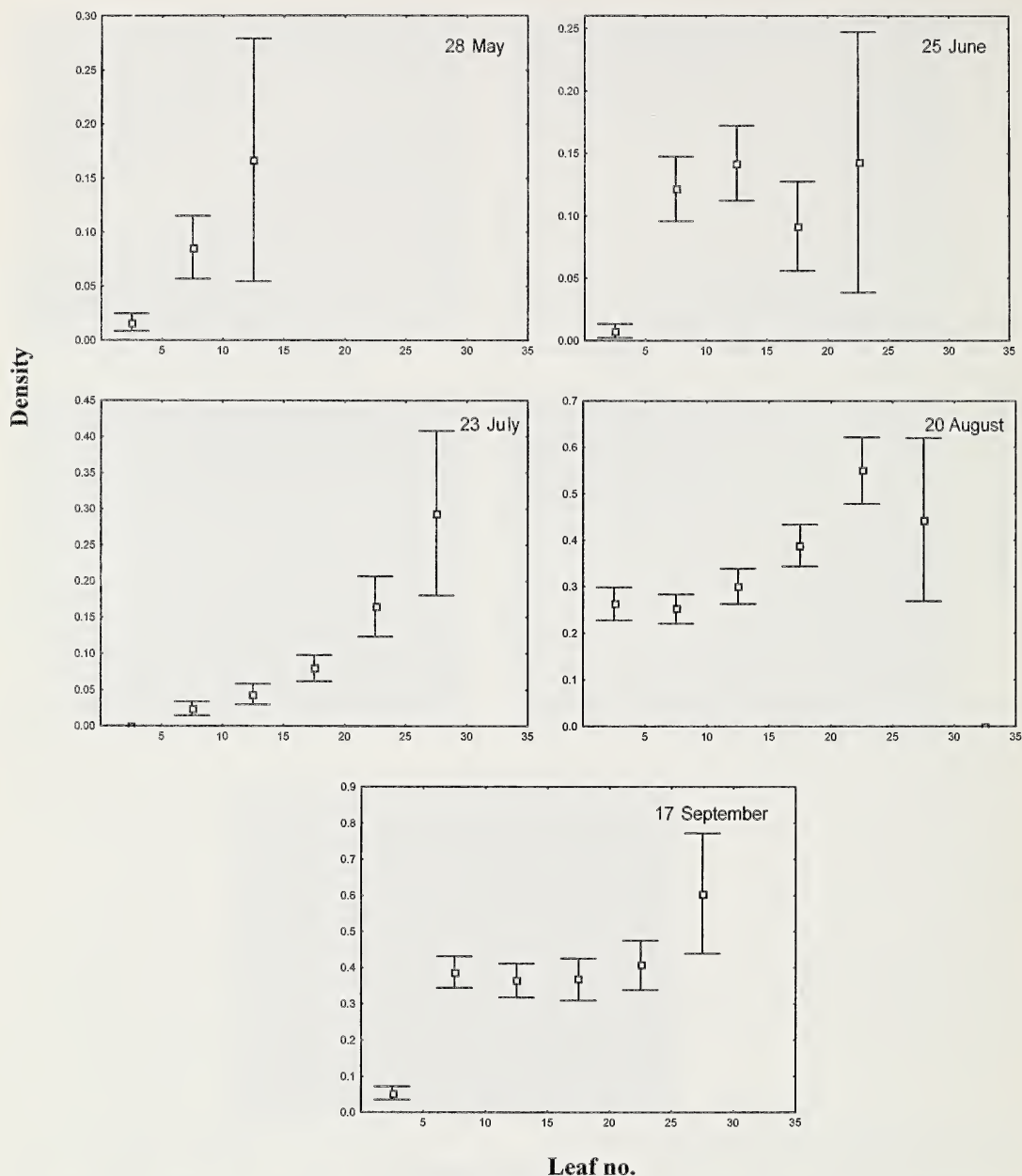


Figure 2.—Seasonal changes in the vertical distribution of spider density (mean  $\pm$  SE) on sunflower plants. Leaves are numbered from the bottom to the top of the plants and grouped into height categories of 5 leaves.

May–June (1.2 times) when the spider density increased on 49% of the plants. From June–July the average density decreased (0.37 times) on 41% of the plants. Finally, from August–September the average density also decreased (0.2 times) on 53% of the plants.

The distribution of spiders changed during the season as follows (Fig. 1): in May, June

and July the distribution was rather random (KST,  $P < 0.01$ ). In August and September it approached a normal distribution (KST,  $P > 0.10$ ). But the analysis of the spatial distribution showed that the distribution was in fact aggregated toward the end of season with two patches of high spider density on the margin of the study plot (Fig. 1).

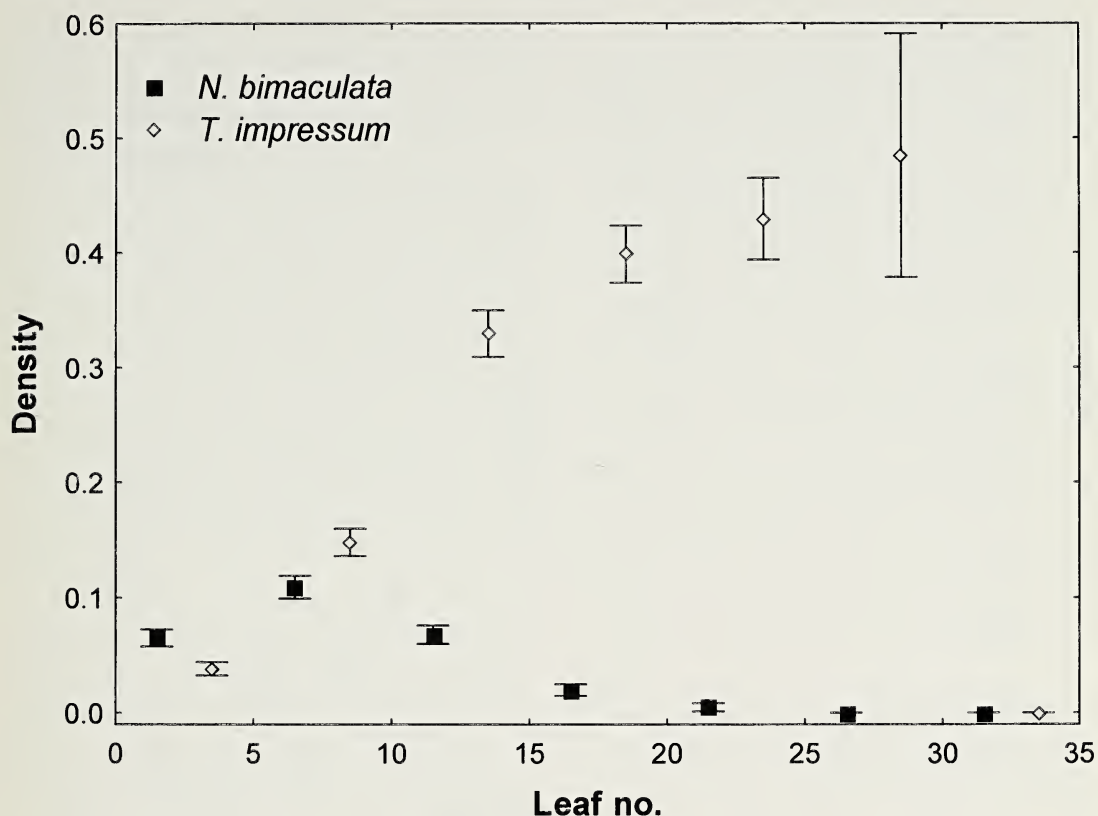


Figure 3.—Mean ( $\pm$  SE) density of *N. bimaculata* and *T. impressum* on sunflower leaves (numbered from the bottom to the top of the plants and grouped into height categories of 5 leaves). Data from July and August pooled.

**Vertical distribution.**—The stratification of spiders did not change dramatically during the season. Temporal analysis showed that the spiders were always more abundant on the upper leaves, except for the terminals, which formed the flower (Fig. 2). The distribution of the two most abundant species, *N. bimaculata* and *T. impressum*, differed. While *N. bimaculata* was mainly found in the lower parts of the plants, *T. impressum* dominated the upper parts (Fig. 3).

The vertical distribution of aphids on sunflower leaves is shown in Fig. 4. Unlike spiders, aphids were more abundant on lower than on upper leaves. The density of spiders (per leaf) was independent of the density of aphids and/or leafhoppers (LM,  $P > 0.23$ ).

#### DISCUSSION

Observed composition of spiders on sunflowers was similar to the canopy fauna of corn, soybean or rape in Europe (e.g., Alderweireldt 1989; Nyffeler 1982), i.e., in all these

studies it was dominated by theridiid spiders. Some differences were observed in comparison with other crops, which presumably result from the different plant structure. Large sunflower leaves do not provide suitable attachments for the webs of araneid spiders, which are therefore more abundant on structurally more complex plants, such as soybean or rape. In North America, the sunflower was dominated by other spider guilds: thomisid and salticid spiders (Seiler et al. 1987). This is because the spider fauna of agroecosystems in North America is different from that in Europe (Nyffeler & Sunderland 2003).

Increase of spider density with the development of crops was observed in many seasonal crops including sunflowers (Royer & Walgenbach 1991; Duffield & Reddy 1997). In this study it was caused by the influx of spiders, mainly theridiids, from neighboring habitats, which is taking place mainly in the spring (Blandenier & Fürst 1997). The new

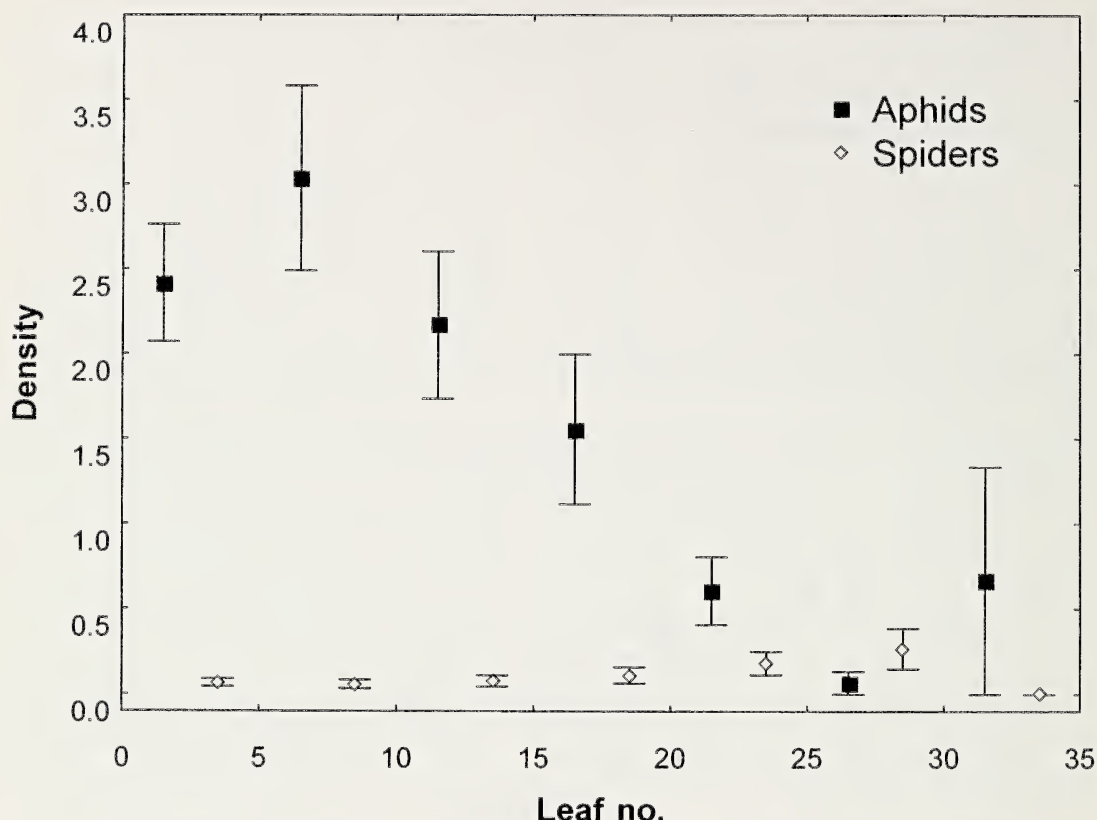


Figure 4.—Mean ( $\pm$  SE) density of spiders and aphids on sunflower leaves (numbered from the bottom to the top of the plants and grouped into height categories of 5 leaves). Data from July and August pooled.

individuals settled randomly in the plot, indicated by their random distribution. In June the spiders reached maturity and mated, followed by a decline in spider density resulting from the death of males. In July they reproduced (Pekár 1999) and the newborn spiderlings dispersed locally. As a result the distribution became aggregated. Such distribution has been rarely documented for spiders in agroecosystems (e.g., Yan 1988; Nyffeler & Breene 1992). Linyphiid spiders showed no evidence of spatial pattern (Thomas et al. 1990; Holland et al. 2004) probably because of their high dispersal ability. A change from random to aggregated distribution as observed in this study was found also by Cang et al. (1989). They recorded that a linyphiid spider *Hylyphantes graminicola* (Sundevall 1830) had a random distribution at low population densities but aggregated at higher population densities in cotton.

Spider densities vary not only temporally but also between different crops. In general,

the density is expected to be a function of plant size and complexity, thus smaller plants host fewer spiders than tall ones. In accordance with this, Liu et al. (2003) observed a maximum density of four spiders per cotton plant, whereas Zhang et al. (1997) found a maximum of six spiders per corn plant.

The two principal species of theridiid spiders seem to utilize different strata for their webs. Such dichotomous but syntopic web placement may be a result of competition or site preference. In an experimental work on the competition between two sympatric linyphiid spiders, Herberstein (1998) found that two species, *Frontinellina frutetorum* (C.L. Koch 1834) and *Neriene radiata* (Walckenaer 1842), compete for web space. As a result, they placed their webs in different strata when occurring syntopically. No web displacement was observed for the theridiid spiders. *Neotitua bimaculata* was never found in the upper strata even on plants where *T. impressum* was absent. Thus it is possible that these two spe-



cies have different microhabitat requirements and do not compete mutually for space. Similar preference for a certain stratum has also been observed in other spider species (e.g. Kim et al. 1989).

In total the number of spiders was higher in the upper than in the lower stratum in this study. In contrast to this, Liu et al. (2003) found that there were more spiders in the lower parts of cotton plants than in the upper parts. Similar results were obtained from a study on rice (Anwaru & Ibrahim 1995). But higher spider densities in the lower strata observed in these studies are due to the inclusion of epigeic spiders. Sunflower plants are not used as foraging sites by epigeic spiders as the leaves are high above the ground so it might be difficult for epigeic spiders to climb sunflower plants.

The number of aphids in this study was higher in the lower strata. Similarly, aphids on chili plants were more abundant in the lower than in higher strata (Idris & Mohamad 2002). Rarely has the distribution of predators in arable land been observed to be spatially dependent on their prey (Wang & Yan 1989). In a study of Holland et al. (2004) linyphiids showed no spatial association with aphids, though being their frequent prey. Pekár (2000) analyzed the diet of *T. impressum* on sunflower. He found it was composed mainly of aphids. Therefore it was expected that the spiders would be more abundant in the lower leaves where aphids were more abundant. But it was not, presumably due to counter effect of other factors, either biotic or abiotic.

#### ACKNOWLEDGMENTS

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## LABORATORY METHODS FOR MAINTAINING AND STUDYING WEB-BUILDING SPIDERS

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**ABSTRACT.** Web-building spiders are an important model system to address questions in a variety of biological fields. They are attractive because of their intriguing biology and because they can be fairly easily collected and maintained in the laboratory. However, the only published instructions for working with web-building spiders are somewhat outdated and not easily accessible. This paper aims to provide an up-to-date guide on how to best collect, keep and study web-building spiders. In particular, it describes how to obtain spiders by capturing them or by raising them from cocoons, how to keep and feed spiders in the laboratory and how to encourage them to build webs. Finally it describes how to document and analyze web building and web structure.

**Keywords:** Data collection, laboratory manual, methodology, spider silk, spider web

Web-building spiders are a popular model system to address questions in various scientific fields such as physiology, ecology, evolutionary biology, ethology and chemistry. Silk production, while not unique to this group, is its most characteristic feature (Craig 1997). Physiologists aim to understand how silk is produced while chemists investigate its properties and structure (e.g., Vollrath 1999; Knight & Vollrath 2001). Webs built out of silk are used to catch insects, making web-building spiders important predators, and even biological control agents (e.g., Riechert 1999; Symondson et al. 2002). As prey remains are often retained in the web post-consumption, prey capture can easily be assessed. The evolution of the web in itself has been studied extensively (e.g., Eberhard 1982; Coddington & Levi 1991; Benjamin & Zschokke 2004). Similarly, sexual cannibalism, prevalent in several families of web-building spiders, or sperm competition and cryptic female choice have been the focus of many exciting studies (see Elgar 1998; Eberhard 2004 for reviews).

Web-building spiders are also attractive to scientists because they can be easily collected and maintained in the laboratory, allowing large sample sizes and large-scale experiments. However, many researchers who rec-

ognize the value of spiders as model systems may be inexperienced in collecting and maintaining web-building spiders. With the present paper we aim to provide the necessary information, in the hope to foster cross-disciplinary studies on these fascinating creatures.

With towards 40,000 described spider species (Platnick 2005), we cannot give specific information for each species. Such information can be obtained either when collecting the spiders in their natural habitat or from researchers experienced with that spider species. Here we focus on species we have worked with, i.e. mainly orb-web spiders, but attempt to make our recommendations applicable to all web-building spiders, especially since much research is still needed on webs of most non orb-web spiders.

### OBTAINING SPIDERS

We recommend obtaining spiders by collecting them in the wild, thereby gaining a first impression of web structure and physical requirements. As most web-building spiders build webs only under favorable weather conditions, they are best found when it is neither raining nor very windy. We do not recommend obtaining spiders from dealers, since the source of these spiders is often unclear and they may be inbred.



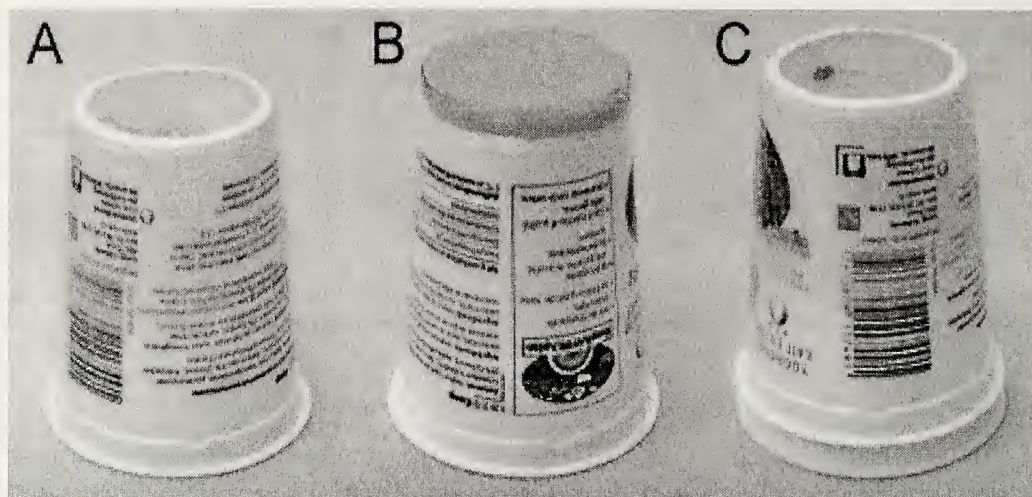


Figure 1.—“Spi-pot”, a simple device to temporarily immobilize a spider for identifying or measuring (modified after Roberts 1995). It consists of two equally sized, round plastic pots. In one pot (pot A), a round hole is cut into its base, leaving a rim of c. 5 mm for rigidity. This hole is then covered with tightly stretched cling wrap, secured along the sides with tape. On the base of the other pot (pot B) a circular piece of soft foam is glued. The thickness of the foam should correspond to the gap at the base when two pots are stacked inside each other. To examine or measure a spider, place it in pot A, push pot B inside pot A and view the spider through the cling film (C).

**Capturing spiders.**—To capture an orb-weaver spider sitting in its web, place a small jar around the spider and replace the cover from the other side of the web. If the web should remain undamaged for photos, tap the web opposite the spider, causing the spider to drop down into a container held below. To capture a spider hiding in a retreat, either collect the entire retreat or lure the spider out of the retreat by placing a vibrating tuning fork on the web (if no tuning fork is at hand, vibrating forceps sometimes also work; Penney 1995). Theridiid and linyphiid spiders may require a larger jar, lifted up quickly from below around the spider in its web. Do not use butterfly nets to capture web-building spiders as this can damage them.

Immature or sub-adults females will have a longer life expectancy than adults and seem to thrive better in the laboratory, whereas adult males do not build webs and adult females may soon start laying eggs, and then build less regular webs. For studying mating behavior, it is essential to control the spiders' mating histories. Unfortunately, identifying sub-adult, live spiders in the field can be difficult or impossible. A good aid to examine live spiders is the “Spi-pot” (Roberts 1995; Fig. 1). For transport, spiders can be housed

in film canisters of 35 mm or APS films. Using the semi-transparent variety, allows checking the spider without opening the canister. Leaves or twigs give the spider a substrate to hang onto and provide some humidity. Place spiders singly in containers to prevent cannibalism.

**Sending live spiders.**—To send spiders by courier or ordinary airmail, put them into a fairly airtight container with a small piece of moist cotton or paper towel to prevent desiccation. The air enclosed in the container is sufficient for many days, and feeding is not necessary during shipment.

**Legal aspects.**—In certain areas or countries, capturing some or all spider species is not allowed or requires permits from the relevant authorities. Similarly, import and export permits and restrictions must be observed when sending or transporting spiders between countries.

**Rearing spiders from eggsacs.**—The easiest starting point to rear spiders from eggsacs are gravid, mated females collected in the field. It is virtually impossible to know whether a female has mated, but the likelihood of collecting a mated female increases with the progression of the season. Unmated females will also eventually lay eggs, albeit infertile



ones. When the spider has built a cocoon, it must be exposed to appropriate climatic conditions, similar to those in its natural habitat. We found it helpful to keep cocoons of various web-building spiders in a chicken egg incubator made of Styrofoam and with a rough temperature control and a water reservoir to maintain humidity levels to prevent desiccation of the cocoons. Unfortunately, eggs often fail to hatch, and even if they do, rearing the spiderlings is a real challenge (see below).

### HUSBANDRY OF SPIDERS

**Enclosures (frames) to keep spiders.**—A variety of frames have been used to study spiders and their webs. In the laboratory of Peter Witt, elaborate metal cages were used (Witt 1971). We suggest simpler frames entirely made out of Perspex. The frame's size should correspond to the web size; initial field measurements may therefore be necessary. To house small to medium sized orb-web spiders (e.g., *Zilla diodia* (Walckenaer 1802), juvenile *Araneus diadematus* Clerck 1757 or *Larinioides sclopetarius* (Clerck 1757)), we used frames consisting of four pieces of transparent Perspex, 5 cm wide, 30 cm long and 3 mm thick, glued together with industrial strength glue at the corners (Fig. 2). Large orb-web spiders (e.g., adult *Argiope* sp.) require frames made out of 50 cm long Perspex pieces and adult *Nephila* sp. require even larger frames. Similar frames, but laid horizontally, can be used for sheet-web spiders (Bartels 1929). Spiders building three-dimensional webs (e.g., linyphiid and theridiid spiders) require cube-shaped frames. For some species it can be advantageous to build the frames higher than wide. To facilitate the spider's grip to the frame's inside, apply net-like crack-seal tape, painted black beforehand to reduce unwanted reflections when later taking pictures of the web. To allow unobstructed examination of the web, the spiders must be kept in frames where two opposite sides can be removed.

To separate the frames, place thin (0.5 mm), large (a few cm larger than the frames), transparent and somewhat flexible PVC sheets between them. These sheets are smeared with Vaseline to deter spiders from attaching threads. Alternatively, windowpanes, which are kept very clean, can be used. In addition, puffy foam can be put along the edge of the frame, encouraging spiders to attach to that

foam rather than to the glass. The frames are put on a shelf like books with the thin sheets placed between them (Fig. 3). When a spider has built a web, its frame can be easily taken from the shelf and placed in front of a shadow box for examination (see below, taking pictures). When handling the frame carefully, the spider usually stays in its web (or retreat). Some freshly caught spiders are likely to leap off the web or leave the hub of the web when their frame is handled for the first time, but will mostly become habituated to being handled after a few days.

There are many alternatives to the durable Perspex frames described above, which may suit short-term or preliminary experiments, such as using rigid cardboard, wooden frames or 'slices' of round plastic buckets with cling wrap to prevent spiders from escaping. Spiders building webs on rather than between supports can be offered an artificial, standardized structure to build their web on (Blackledge & Wenzel 2001), which is then placed inside a larger container with clean, smooth sides.

For short-term storage of smaller spiders we use upturned plastic cups from which the bottom has been removed and replaced with a fine mesh. Smaller spiders will build small webs in these cups, which can be misted from the top (with a spray bottle) without lifting the cup. Alternatively, only a small hole is cut into the bottom of the cup and corked with a cotton plug or a tampon piece. Water is then administered by wetting the cotton plug. Keeping spiders in such small cups can also be an experimental procedure; e.g., when studying web-building behavior, larger spiders can be maintained in cups to temporarily prevent them from building webs (e.g., Reed et al. 1970; Herberstein et al. 2000).

**Feeding and watering.**—Spiders can be fed with almost all kinds of insects, and most web-building spiders will attack and overwhelm insects trapped in their web in a large range of sizes, up to their own size or even larger. *Drosophila* flies are often used, as they are easily reared. When rearing *Drosophila* in bottles with sponge stoppers, spiders can be fed by trapping single flies between the flange of the stopper and the bottle, from where they can be introduced into the web using forceps. Spiders without webs are trickier to feed; some spiders accept live prey held near their mouth with forceps; buzzing flies are more

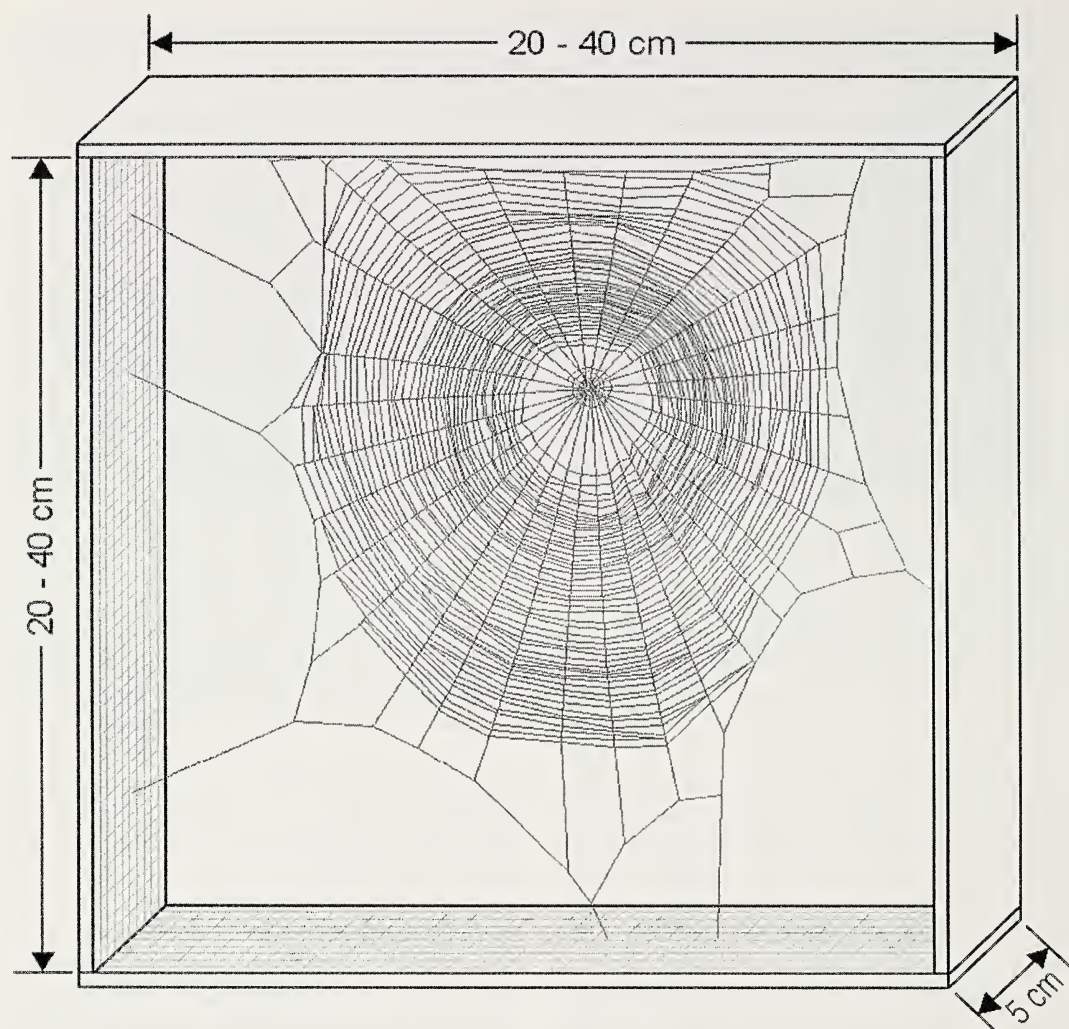


Figure 2.—Frame to keep orb-web spiders made out of four Perspex strips, glued together at the corners (not to scale). On the inside of the frame, blackened crack-seal tape has been applied to facilitate the spider's grip. Similar frames with dimensions accordingly adapted can be used for other web-building spiders.

readily accepted than kicking crickets. Sprinkling water over the offered insect or breaking the insect's cuticle a bit by snipping a cercus or antenna to release a drop of hemolymph can induce spiders to feed when the liquid touches the spider's chelicerae. It is sufficient for most spiders to be fed once per week. However, since feeding spiders without web can be tricky, we recommend feeding spiders twice per week. Feed spiders at least so much that they do not lose substantial amounts of weight, causing their abdomens to shrink. Whereas some spiders can be kept for a prolonged time on such a minimal diet (in our

experience e.g., *Araneus diadematus*, *Zygiella x-notata* (Clerck 1757)), other species seem to falter when they are not given enough food to grow (e.g., *Argiope bruennichi* (Scopoli 1772)). Natural prey capture rates may provide helpful starting points when designing feeding regimes in the laboratory. It is important to either feed the spiders with different insects or to feed the prey insects with high quality food (i.e. supplemented with proteins, vitamin-enriched cereal or pet food), as the spiders may otherwise experience deficiencies (Uetz et al. 1992; Mayntz & Toft 2001). The relatively dry air in most buildings makes spi-



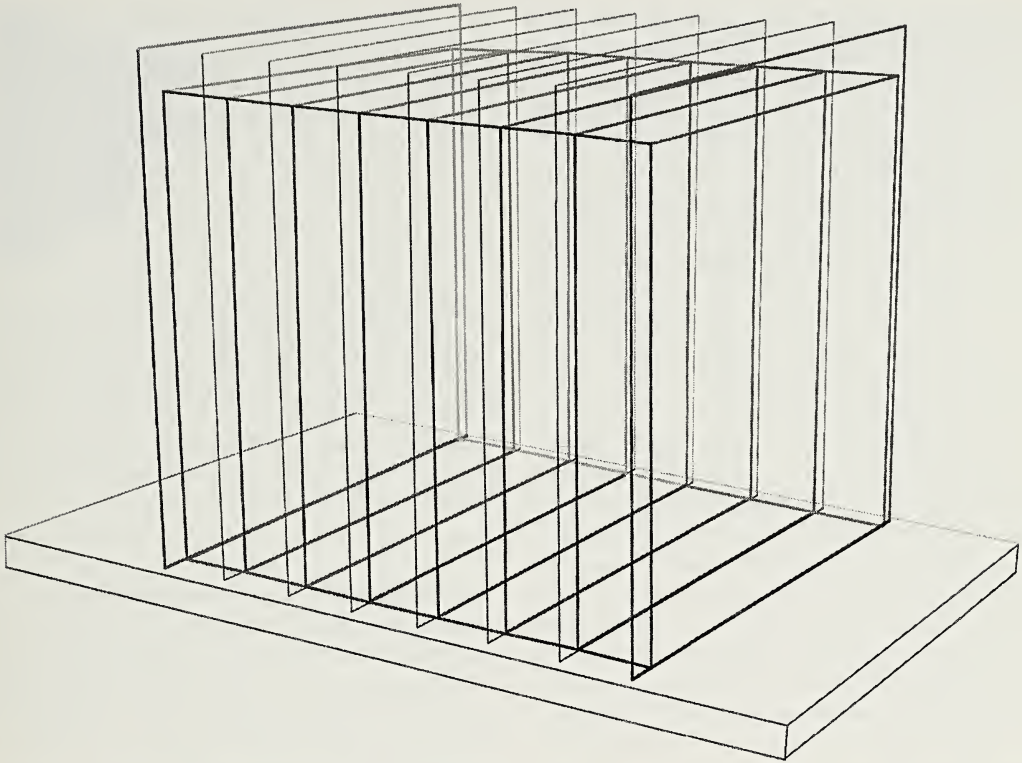


Figure 3.—Several frames (cf. Fig. 2) put side to side on a shelf. Thin PVC sheets placed between adjacent frames prevent the spiders from moving between frames. The thin sheets are smeared with Vaseline to prevent the spiders from attaching threads. The first and the last sheet are thicker, more stable ones, held up with bookends (not shown).

ders kept inside vulnerable to desiccation. Thus regular misting with a water sprayer or placing a moist sponge at the bottom of the frame is vital. For experiments on the impact of drugs or pesticides on web building consult earlier studies on how to administer drugs (e.g., Witt et al. 1968; Witt 1971; Samu & Vollrath 1992; Hesselberg & Vollrath 2004).

**Rearing spiderlings.**—This is notoriously difficult and fraught with high levels of mortality. To rear spiderlings, place the freshly hatched cocoon into a container with support for the webs such as wood-wool, and add cultures of *Drosophila* or Collembola as food (Dinter 2004). Initially, some spiderlings will consume each other; more established ones then construct webs and capture prey. Do not separate the spiderlings too early as this can lead to almost total mortality.

**Encouraging web building.**—Spiders vary greatly in their propensity to build a web in the laboratory. It is possible to find out which spider species build webs readily by identi-

fying species used in earlier laboratory studies. The most popular orb-web species include *Araneus* sp., *Argiope* sp., *Nephila* sp. and uloborid spiders. In contrast, *Gasteracantha* sp., *Tetragnatha* sp., *Meta* sp., *Metellina* sp. and *Leucauge* sp. are more hesitant to build webs. Feeding a spider that has not yet built a web in the laboratory, or putting a live fly into the cage together with the spider (Pasquet et al. 1994) can help to induce web building. If releasing a live fly into the frame with the spider is problematic because of strict feeding regimes, flies can be kept in a small jar with some sugar solution and covered by fly mesh. This way the flies buzz and stimulate web building without being captured by the spider (Herberstein et al. 2000). Web building frequency is also higher when spiders are exposed to natural day—night cycles in light and temperature (Witt 1956).

Once the spider has built its first web in the laboratory, feed it soon to encourage the spider to build again. Web building frequency

varies between species. Whereas *Araneus diadematus*, *Argiope* sp., *Larinioides sclopetarius* and *Zygiella x-notata* generally rebuild the capture area of their web every night or every other night, *Nephila* sp. typically rebuild only sections of the web.

**Damaging webs.**—Some orb-web spiders hesitate to rebuild their web as long as it is intact. To induce web rebuilding, it may therefore be necessary to damage or destroy the webs. In the field, spiders generally leave the frame and the anchor threads largely intact when rebuilding the web (Carico 1986). Thus, only the capture area should be damaged to induce rebuilding, e.g., by cutting holes into the capture area with a red-hot wire (Fig. 4). Alternatively, cut the lateral anchor threads with scissors to destroy the entire orb-web. However, complete web destruction forces the spider to build the next one from scratch, which can influence aspects of the web (Zschokke & Vollrath 2000). In general, the spider should be allowed to ingest the old web (Peakall 1971). Damaging a single sticky spiral segment allows to determine whether the spider rebuilds the web during the next night.

Non orb-web spiders do not remove, ingest and rebuild their web as orb-web spiders do, but keep repairing and extending them (Tanaka 1989; Benjamin & Zschokke 2003, 2004). To study the construction of these webs, remove the old web completely or place the spider in a new frame.

#### DATA COLLECTION

**Observing web building.**—Observing spiders during web building is not easy because they are very sensitive to disturbance, especially during the early stages of web building (which are therefore least well known; Zschokke 1996) and because the time of web building is generally during the night but otherwise largely unpredictable, likely depending on changes in temperature or light (Spronk 1935; Witt 1956). Observing web building is additionally impeded by the light sensitivity of most web-building spiders. Again, spiders differ in their sensitivity. *Araneus diadematus*, *Nephila plumipes* C.L. Koch 1839 and *Argiope keyserlingi* Karsch 1878 are fairly tolerant to some light and may even rebuild their web during the day, whereas other species (e.g., *Nuctenea umbratica* (Clerck 1757), *Zygiella x-notata*) will only build in absolute darkness.

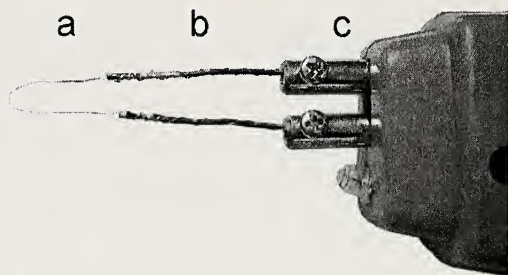


Figure 4.—Tip of a modified soldering gun used to selectively damage parts of a web. The thick wires (b) emerging from the front of the soldering gun (c) are either parts of the original tip or wires as found in 220 V wires. Soldered to these thick wires is a single strand of a 220 V cable (a). To ensure good contact between wire and strand, the strand is wrapped around the wire.

These difficulties can be overcome by using automated spider tracking under infrared light (Benjamin & Zschokke 2002). This method additionally records the spider's time budget, but neither records the position of threads nor all details of the spider's behavior.

**Taking pictures.**—Since spider web silk is very thin (c.  $0.5\ \mu\text{m}$ – $5\ \mu\text{m}$ ), taking pictures of spider webs with all threads clearly visible is difficult. Earlier studies suggested placing the entire web in a box filled with ammonium chloride (Peters et al. 1950) or coating it with white glossy spray paint (Witt & Reed 1965) to increase thread visibility. However, these approaches require removing the spider from the web, they may distort the web and prevent spiders from ingesting the web, as orb-web spiders usually do (Peakall 1971), or to keep using it as non orb-web spiders do. Good pictures of spider webs can also be obtained with untreated webs. The main requirements are bright light from the sides and a very dark background, such as a shadow box lined with black velvet (Langer & Eberhard 1969; Zschokke 2002). We obtained satisfactory results using two 15W fluorescent bulbs on either side of the web with an aperture of 4.5 and an exposure of 1 sec. when using a 55 mm lens on a SLR camera loaded with 100 ISO B/W film (Agfapan). To further improve picture quality, add two bulbs along the top and the bottom of the web. When using a digital camera, a good resolution (at least 3–4 Megapixels) is essential. Since the picture is mostly dark, with fine white lines, use manual



settings, as the automatic settings of most cameras will produce inferior to unusable results. Every photograph should be recorded in a lab book and, to avoid any possible confusion, include a marker along the edge of the picture for identification, together with a scale and an indicator for the top of the web.

**Describing webs.**—Several approaches have been proposed to estimate the area of orb-webs (Herberstein & Tso 2000 for *Argiope* sp. webs and Blackledge & Gillespie 2002 for webs of *Cyclosa* sp. and *Tetragnatha* sp.), as well as the total thread length as a measure of the spider's investment (Heiling et al. 1998 for *Larinoides sclopetarius* webs and Venner et al. 2001 for *Zygiella x-notata* webs). These approaches require measurements of various web parameters, including number of spiral turns, and capture and hub area dimensions. Their suitability depends on the web shape, and whether field or laboratory measurements are made. Field measurements are difficult and it may be wise to select a formula requiring only few measurements; a reduced measuring accuracy can be compensated with a larger sample size (Zschokke & Lüdén 2001). Even though measurements in the laboratory are easier and more precise, these formulae only provide estimates. To obtain accurate data, take a photograph of the web (see above) and import it into a graphics program that calculates area or thread length digitally.

In the past, a multitude of names have been used for the various parts of webs. To avoid confusion, use established names (Zschokke 1999 for orb-webs). Similarly, with names of some spider species changing over the years, make sure to use the current species name (Platnick 2005).

**Measuring spiders.**—Spider size refers to the length or width of a sclerotized body part, such as leg length (typically the tibia-patella length of the first leg is used) or carapace width. As these parts do not grow between molts, they provide information on the growth rate prior to the previous molt; and they can be relevant web parameters (e.g., leg length can influence mesh size in orb-webs; Vollrath 1987). Live spiders need to be immobilized for measuring with a Spi-pot (see above) or with CO<sub>2</sub>. When using CO<sub>2</sub>, gently blow CO<sub>2</sub> into a sealable jar with the spider until the spider stops moving; taking care not to kill the spiders with too much CO<sub>2</sub>. Large spiders

can be measured with electronic calipers, small ones under a dissecting microscope with an ocular fitted with a reticule. Keeping the exuviae of the spiders allows later size measurements. Spider weight is also an informative and fairly easily obtained measure. Weight in addition to size can then be used to estimate recent foraging success by calculating spider condition (weight / size or residuals of weight / size; Jakob et al. 1996; Kotiaho 1999).

## CONCLUSIONS

Web-building spiders provide excellent models to test general and spider-specific hypotheses. Collection and maintenance of juvenile and adult spiders is relatively easy, ensuring large sample size and power. While rearing juveniles from eggs is difficult, some research groups have achieved relatively high rates of survival. Manipulation and observation of web-building spiders in the laboratory is simple and can be achieved by non-arachnologists by following some basic rules set out above.

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## THE LIFE HISTORY OF *YLLENUS ARENARIUS* (ARANEAE, SALTICIDAE)—EVIDENCE FOR SYMPATRIC POPULATIONS ISOLATED BY THE YEAR OF MATURATION

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**ABSTRACT.** The lifespan of *Y. arenarius* is about 720 days for males and 750 days for females (maximum 770 days), which makes it the longest lived salticid reported from natural conditions. The juvenile spiders emerge at the beginning of June and mature not before the following August. They mate in autumn and hibernate for the second time. For most of the year two cohorts coexist, and at the beginning of June three cohorts can be found simultaneously. The life cycle suggests that in the studied areas there are two groups of individuals, the first of which produces young in odd years, while the other group reproduces in even years. The spider lifespan and phenology suggest no or limited gene flow between the groups.

**Keywords:** Salticidae, life history, sympatric populations, isolation, *Yllenus arenarius*

Spider life histories have received considerable attention, which has led to some general attempts at life cycle classification and understanding the factors responsible for cycle control, and for growth and development of spiders (rev. in Schaefer 1987; Vollrath 1987). The specific knowledge of life cycles is, however, restricted to some groups, while others remain poorly known.

The knowledge of salticid life cycles is very scarce. The spiders are relatively small and occur in low densities, so they have attracted little interest concerning both general biology and ecology (Wise 1993). Since the works published by the end of the seventies (e.g.: Horner & Starks 1972; Edwards 1975; Jackson 1978) few papers on the topic have appeared (e.g.: Matsumoto & Chikuni 1987). Instead, salticids have recently been the subject of intensive behavioral studies (rev. in Jackson & Pollard 1996) and some species have gradually become models in studies of invertebrate cognition (e.g.: Wilcox & Jackson 1998). The knowledge of the model's general biology is often, however, essential for the proper interpretation of ecological and behavioral data.

Jumping spiders are commonly characterized as possessing stenochronous life cycles (Schaefer 1987). From particular studies car-

ried out on species occurring in temperate climate we know that they have annual or biennial life cycles (e.g.: Horner & Starks 1972; Jackson 1978; Matsumoto & Chikuni 1987). Such information can also be deduced from the occurrence of sexually mature individuals, which is sometimes given in local keys (Prószyński 1991).

The current work aims to describe the life history of *Yllenus arenarius* Menge 1868, which is a medium-sized jumping spider with an adult body length of about 7 mm. Typically for Salticidae, sexual dimorphism is poorly marked in body size but distinct differences are exhibited in coloration. It is known only from Central and Eastern Europe with the westernmost localities in NW Germany and the easternmost on the river Volga (Prószyński 1991; Logunov & Marusik 2003). The spider inhabits sandy dunes along rivers as well as inland and coastal dunes. In the habitats it is restricted to the initial stage of the *Spergulo-Corynephorum* and tends to keep away from dense vegetation (Żabka 1997; Bartos 2000; Merckens 2002).

*Yllenus arenarius* is a polyphagous salticid preying on a wide spectrum of invertebrates (Bartos 2004). It is also known for its conditional hunting tactics flexibly adjusted to prey type (Bartos 2000, 2002a). Another interesting



fact concerning the spider's biology is its unusual sub-sand nests built for various purposes: molting, egg-laying, surviving the period of night and hibernating. The nest types differ according to their size, shape and general structure (Bartos 2002b).

## METHODS

**Study period and area.**—The research carried out from 1998–2003 encompassed 14 populations from Central and Eastern Poland. One of the sites (Kwilno), located in Central Poland about 25 km to the north of Lodz, was visited at least every two weeks during the vegetation season. Data from the other sites were collected more occasionally, but with respect to spider phenology and body size they were consistent with the data from Kwilno and therefore they were pooled.

**Morphometric measurements and phenology.**—Spiders were collected by means of visual searching through the dune surface between 10:00 and 12:00 hours. During each field visit it was attempted to collect at least 40 individuals (10 juveniles from each cohort, 10 females and 10 males). Spiders from all age groups show the same pattern of variation in activity during the day, therefore the samples seem to be representative for the whole population (Bartos pers. obs.). In anticipation of hatched juveniles or adults after the final molt the field was visited every day starting at least ten days before the expected time.

Three measurements of live specimens were taken with a stereomicroscope (precision: 0.01 mm) ( $n = 1208$ ): abdomen length (AL), abdomen width (AW) and posterior eyes width (PEW). To immobilize the spiders during the measurements they were covered with a transparent kitchen foil and delicately pressed against a piece of sponge. Sex and age of the spiders were also recorded. The characteristics allowed to include the spiders to certain age groups (Figs. 1–3).

**Winter samples.**—In winter a two-centimeter thick layer of sand was collected from the dune surface and dried in the laboratory (temperature at ca 25 °C). Spiders, which emerged from the sand were collected, measured and subsequently reared until they died. The dried sand was also sieved to collect nests and immersed spiders. Air temperature at the level of the sand surface was measured with an alcohol thermometer (precision: 0.2 °C).

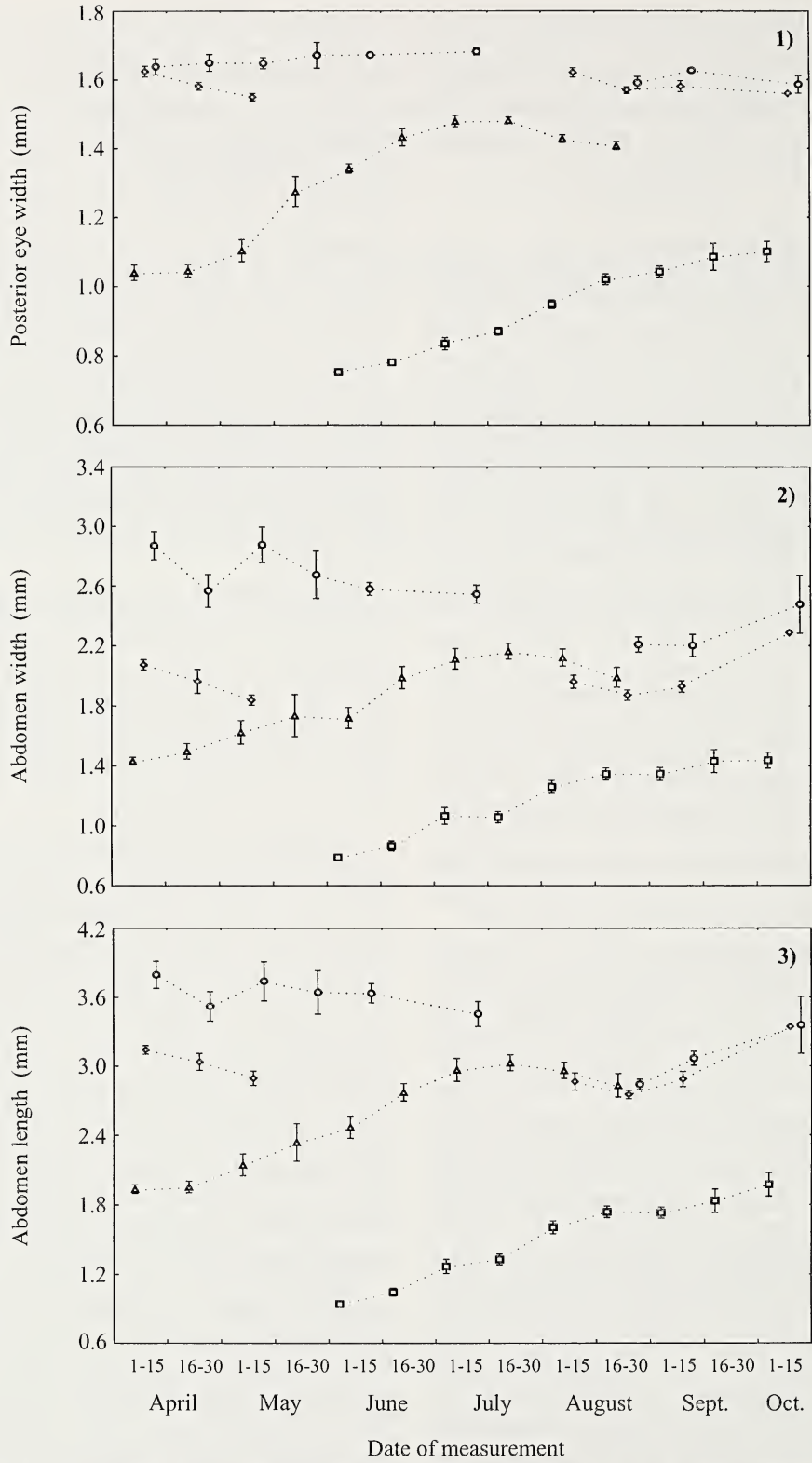
**Rearing.**—Females were kept in the laboratory to estimate the number of eggs, the period of egg laying and determine the place where they are laid. Spiders were reared individually in glass containers (1 liter) with a three centimeter-thick layer of dune sand on the bottom. Temperature was maintained at ca 25 °C, light regime 12L:12D and the sand was moistened weekly with 5 ml of water. They were fed ad libitum (10 fruit flies twice a week). Under these conditions 26 females were kept. Six females came from winter sand samples and the rearing started in February, while 20 other females were collected at the beginning of April. The sand from the laboratory containers was sieved every two weeks in order to collect nests. The nests were opened and checked to find eggs and exuviae. The individuals in the laboratory survived until mid June.

**Data analysis.**—All statistical procedures followed those described by Zar (1984). The significance of the differences in body length parameters was tested with one-way ANOVA and Tukey test with unequal sample sizes. Data are presented as mean  $\pm$  SD ( $n$ ) except for Figs. 1–3 which present mean  $\pm$  1.96 SE.

## RESULTS

**Morphometric measurements and phenology.**—Taking into account the season in which the spiders were collected, spider size and maturity, four age groups were distinguished (Figs. 1–3): juveniles in the first season of life (juv-I), juveniles in the second season of life (juv-II), which underwent maturation in August, adults in the second season of life (ad-II) and adults in the third season of life (ad-III). In each of the studied seasons two spider cohorts were observed for the whole season (either juv-II and ad-III or juv-I and juv-II/ad-II) and, in June, spiders from all three cohorts were observed simultaneously (juv-I, juv-II and ad-III).

Spiders from the same cohort were observed for three consecutive years (Figs. 1–4). Males were found even up to 720 days from leaving their sub-sand nests. The latest recording time for females ( $n = 3$ ) was 15 July in 1998 and 2003. Their lifespan, calculated from the time of emerging from the sub-sand nest, is about 750 days. The females, however, were numerous only by the begin-



Figures 1-3.—Changes of three morphometric parameters in the life cycle of *Yllenus arenarius*. 1. Posterior eyes width; 2. Abdomen width; 3. Abdomen length; squares, juv-I ( $n = 573$ ); triangles, juv-II ( $n = 363$ ); diamonds, males ( $n = 124$ ); circles, females ( $n = 148$ ); symbols are means; error bars are 1.96 SE.



ning of June. Later only scattered individuals were recorded.

Spiders of all age groups were active from the first 10 days of April to mid October as long as the air temperature measured on the dune surface was above ca 10 °C. Spiders were never found when the temperature was lower than 10 °C. Therefore, because of overall harsh autumn weather conditions, in most seasons of study they disappeared before the end of September, rarely at the beginning of October (Figs. 1–3). On several warm winter days in February, however, several females were found hunting on the dune surface (at temperature 11.4 °C). All age groups started their activity at the same time in spring and were also found to burrow almost simultaneously for hibernation in autumn.

*Juveniles in the first season of life (juv-I):* During three study seasons, when the newly emerged juveniles were searched for, they appeared within almost the same period of time (between 3 and 6 June). Their body length was about  $1.87 \pm 0.14$  mm ( $n = 30$ ), they had semitransparent carapace and their round cephalothorax and abdomen closely resembled the dune sand grains in color, size and shape. Shortly after emergence the spiderlings were found in groups of up to six individuals remaining only a few meters from each other, which suggests that they emerged from the same sac. Later, when the spiders started to disperse, they were rather evenly distributed over the dune. However, even a week after the first juveniles appeared on the surface, some groups consisting of a few spiderlings were also found, which suggests that they had just left the hatching chamber. Juveniles in the first season of life were observed throughout the summer until the beginning of October, when the first hibernation started (Figs. 1–3).

*Juveniles in the second season of life (juv-II):* The spiders finished their hibernation at the beginning of April. In mid June the distal parts of the pedipalps of some juveniles began to swell, which made it easy to determine them as subadult males. They reached the subadult stage at different times and swollen pedipalps were commonly observed in subadult males only in mid July. Other characteristics of both sexes prior to final molting were indistinguishable. Spider color and body pattern, so different in adult males and females, were identical in subadults. In the last week of July

almost all juveniles in the second season of life burrowed to undergo the final molt in their sub-sand nests. The first to disappear, however, were subadult males. At that period only juv-I were commonly found on the surface. Such pattern of simultaneous disappearing of almost all individuals from a cohort, while the other cohort did not show apparent differences in number, was observed several times in the field. However, such absence was recorded for only a few days, which cannot be presented in the two-week-long periods in the figures.

*Adult spiders:* The first adults to appear were males, observed as early as 8 August. During all three years, when the first mature males were particularly searched for, they appeared regularly between 8–10 August. The first adult females were observed at least ten days later. Male coloration and body pattern changed significantly after the last molt. Generally, after the last molt males became much more conspicuous and easy to spot while female cryptic coloration remained unchanged. Female coloration also changed throughout their mature life mainly due to losing scales in the course of burrowing. In June, i.e. after 10 months from the last molt they were much darker, with patches of black cuticle visible in the areas where the scales were missing. In extreme cases the dorsal area of their abdomen was black. This makes them unmistakable from freshly molted females.

Not only general appearance, but also some body measurements of adult females changed over their mature life (Figs. 1–3). There were no differences in posterior eyes width (Fig. 1) ( $F_{8;143} = 1.38$ ,  $P > 0.05$ ). Such differences were found, however, for abdomen length ( $F_{9;137} = 4.89$ ,  $P < 0.001$ ) and abdomen width ( $F_{9;139} = 5.71$ ,  $P < 0.001$ ). Freshly molted adult females had on average shorter abdomens than those in the next spring by the end of May (significant at  $P < 0.05$ ), but not the females in the second half of April ( $P > 0.05$ ). A similar tendency was observed for abdomen width, being thinner in females shortly after the final molt in comparison with those in the first half of April and in the first half of May ( $P < 0.05$ ), but again no differences with females in the second half of April. The latter group had on average shorter abdomens than the females directly before and after the period ( $P < 0.05$ ).

In the group of adult males the differences

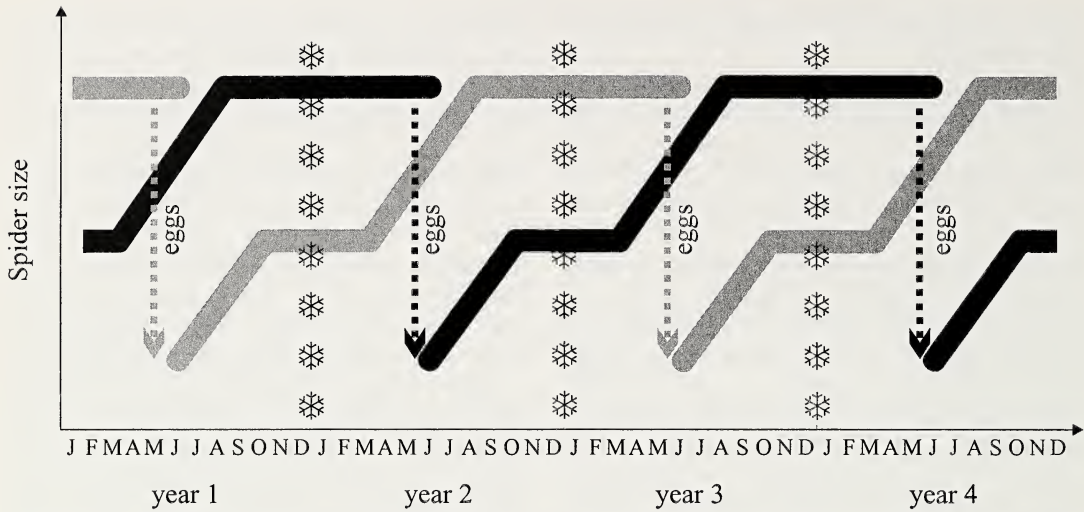


Figure 4.—Schematic presentation of the life cycle of *Yllenus arenarius*. grey bars = spiders hatching in odd years; black bars = spiders hatching in even years.

were found only between those measured in the second half of August and early next spring. The first group was larger than the second according to posterior eyes width ( $F_{6;121} = 3.01$ ,  $P < 0.01$ ) (significant at  $P < 0.05$ ), abdomen length ( $F_{6;109} = 8.38$ ,  $P < 0.001$ ) ( $P < 0.001$ ) and abdomen width ( $F_{6;109} = 4.17$ ,  $P < 0.001$ ) ( $P < 0.005$ ).

**Winter samples.**—In winter sand samples collected in February at ambient temperature of  $-8^{\circ}\text{C}$  and under ten-centimeter-thick snow cover, 26 live individuals were found. These were juv-II ( $n = 12$ ), ad-III ( $n = 14$ ): eight males and six females. Spiders from all age groups hibernated successfully. Spiders were found in only one out of four sand samples. Two spiders were found in elongated nests impregnated with organic matter, while the other individuals were being active at the time and were collected from the sand surface. Their winter nests were found after sieving the sand.

**Rearing.**—Females reared in the laboratory ( $n = 26$ ) laid on average  $6 \pm 0.8$  eggs ( $n = 5$ ). The eggs were spherical or slightly oval, on average 1.20 mm in diameter ( $\text{SD} = 0.17$  mm,  $n = 4$ ). In all cases the eggs were laid in one batch only. The nest in which eggs were laid was different from other nests found in the same container. It possessed a specific structure. It was made of dense silk and sand grains and possessed two chambers. Eggs were attached to the wall with a sheet of silk slightly pressing them to the wall. Inside, the

eggs and empty chorions were found. The spiderlings hatched in a small chamber of the nest, and molted for the first time in the big chamber, where their exuviae were found.

The actual process of egg-laying was not observed since it takes place inside an opaque, underground nest. For this reason the date of egg-laying in the field is also unknown. However, one of six females found in winter sand samples laid eggs in laboratory conditions after about two weeks from interrupting its hibernation. About four weeks later spider nymphs emerged from the underground nest. The spiderlings in laboratory performed burrowing behavior and built oval, thin-walled sub-sand nests soon after their first appearing on the surface.

DISCUSSION

The life history analysis suggests, that the lifespan of *Y. arenarius* counted as the time from leaving the sub-sand nests to the last individuals observed in the field is about 720 days for males and 750 days for females (maximum 770 days), which makes it the longest-lived salticid reported from natural conditions (Jackson 1978; Horner & Starks 1982; Matsumoto & Chikuni 1987). There are reports of *Sitticus fasciger*, which lived over 800 days in the laboratory, but only up to 428 days in the field (Matsumoto & Chikuni 1987). From the exceptional variability in the rate of development and lifespan of spiders



(e.g.: Turnbull 1962; Toft 1983) we may expect that the lifespan of the studied spider may also be variable, as local weather conditions and food availability fluctuate.

The life cycle of *Y. arenarius* is characterized by an at least potentially long reproductive period, which may last for about two months in autumn and for another two months the next spring. Copulating spiders were, however, found only in autumn. The possible reason is, that as time elapsed, females were getting less receptive (Bartos pers. obs.) and male condition was also getting worse, especially in spring (Figs. 1–3). Therefore most likely copulation occurred in autumn and egg-laying took place the following spring.

The spiders most probably lay a few large eggs in one batch. Laying multiple batches in the field cannot be excluded, however. Large egg dimensions in comparison to the largest female's abdomen size (Figs. 2, 3) suggest that the total number of eggs laid at one time must be close to the number observed in one batch. Semelparity is also suggested by rather uniform size of spiderlings (at least during the first few months). If there were more than one clutch, they would have to be separated by 1–4 weeks and as a result the spiderlings would differ in condition and size (Horner & Starks 1972; Jackson 1978; Matsumoto & Chikuni 1987), which is not the case here (Figs. 1–3).

Even though the exact period of egg laying cannot be directly indicated, it may occur either in mid April, when female abdomens rapidly shrink or in mid May. At the beginning of this month female abdomens are the largest in the whole life cycle (Figs. 2, 3). No such tendency was observed in average posterior eyes width (Fig. 1), which suggests that the group of measured females did not differ in overall size but only according to their abdomen size. Even though there are two periods when female abdomen shrinks, which may suggest egg laying, the process most likely occurs in May, which is about a month before a new cohort emerged. This is consistent with average period of egg development and nest residence by spider larvae and nymphs (Horner & Starks 1972; Jackson 1978; Matsumoto & Chikuni 1987). The early period of female abdomen shrinking is possibly due to low prey availability, prey becoming more numerous only in late June after juveniles leave their nests (Bartos pers. obs.). Such synchroniza-

tion of egg-laying with food availability has been commonly reported (Almquist 1969; Schaefer 1987). Underground nest location with no signs of repeated nest visiting (Bartos 2002b) imply the lack of brood care.

Life history traits of *Y. arenarius* such as low fecundity and relatively large eggs, slow development, delayed reproduction, long life span and a degree of territoriality (Bartos pers. obs.) place this species as a K-selected organism, well adapted to the unfavorable environment. As one of major predators, outnumbered only by ants (Bartos pers. obs.) it seems to be a successful competitor in the environment. Apart from the spiders' cryptic coloration, the key adaptation to survival in the cover-free habitat seems utilization of underground space, i.e. the burrowing and underground nest building, so typical for many animals dwelling in arid environments (e.g.: Gwynne & Watkis 1975; Cloudsley-Thompson 1983; Henschel 1990). Underground nests provide the spiders with more stable conditions, shelter against night active predators, strong wind and periods of inclement weather such as heavy rains, which may be a severe mortality factor. The importance of the nests is also suggested by the number of nests built especially by juveniles. In the laboratory the juveniles built nests daily, which is significantly more often than in subadults and adults (Bartos 2002b). Such a high rate of nest building in juveniles connected with silk production and apparently energy-demanding underground nest building must be an important expenditure in the energy budget at the expense of other processes, e.g. growth and development.

Morphological and phenological data suggest that the spiders lay eggs two years from the time they hatch. However, in the field, newly hatched spiders are found every year. This suggests that in the dunes of Central and Eastern Poland, there are two sympatric populations of *Y. arenarius* reproducing in odd and even years (Fig. 4). Phenology of males and females in the field suggests that there is no gene flow between the groups or it occurs accidentally and must be limited. Gene flow may take place if adults from one cohort in spring survive until they meet sexual partners from the other cohort in August. This is very unlikely, though not impossible. Males would have to live for another two months and fe-



males for one month longer than the most long-lived individuals in the field. This was not observed in the period of studies since very characteristically looking old females were never recorded after mid July. For females such prolonged survival would also mean to live even longer, for another nine months until the next spring (and hibernate for the third time), when eggs are laid and young were found to emerge from egg sacs.

The apparent reproductive isolation may be, however, incomplete if at least a small proportion of the population reproduces every year or every three years or the immigration from population of an annual cycle (if there is one) occurs. Such phenomena were reported for several spider species (Toft 1976, 1983) and in the recent research on the reproductive isolation of *Araneus diadematus* were the most probable causes of the lack of genetic differences between markedly separated generations (Johannessen & Toft 2002). Another potential cause of gene flow between successive cohorts may be prolonged hibernation or aestivation. However, it seems very unlikely since it would require surviving several months while being immersed in hot and dry sand. The temperature at the depth the nests are built exceeds 50 °C in hot summer days (Bartos pers. obs.). On the whole, no evidence supporting the alternative scenarios were gathered over the period of studies. Interestingly a very similar phenomenon of two sympatric groups isolated by the season of reproduction was described in another salticid, *Sitticus fasciger* (Matsumoto & Chikuni 1987).

It is curious how such a pattern evolved in the first place. Certainly not as a result of the appearance of early and late maturing adults (Schaefer 1987), since we would then find slowly and quickly developing individuals. Instead we observe relatively uniform growth in the whole cohort of individuals.

Two hypotheses seem to be most likely: a) if all populations of *Y. arenarius* require three seasons for development, then a part of them might have been shifted by one season and later mixed with the original group, b) if southeastern populations have shorter cycles, then repeated migrations might have resulted in the pattern observed. Both hypotheses assume two allopatric populations, which possessed cycles shifted from each other by one year. After mixing they formed sympatric

groups isolated by the year of reproduction. Whichever hypothesis is correct, the life cycle pattern we can observe now is probably indebted to the well-known variability of spider rate of development depending on local conditions (Schaefer 1987) resulting in prolonged or shortened cycles (e.g.: Jackson 1978; Toft 1983).

Another interesting question for speculations is: when did it happen? Nowadays this stenotopic species inhabits most commonly well isolated dunes. Ballooning has never been observed and seems an unlikely way of reaching another dune, which is a rare habitat not only in Poland, but in all Europe. Sandy areas were, however, more common in the past. So, did the switch happen as long ago as the time after the last glaciation, when bare moraine sands were common in Central Europe? The author hopes that planned studies will help to test these hypotheses.

#### ACKNOWLEDGMENTS

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## SPATIAL ASSOCIATION BETWEEN A SPIDER WASP AND ITS HOST IN FRAGMENTED DUNE HABITATS

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**ABSTRACT.** In patchily distributed habitats, species potentially occur wherever conditions are suitable or show a restricted distribution, influenced by patch quality, geometry and configuration. If patch isolation appears to be the main determinant of the species' distribution then dispersal ability is supposed to be limited. Although only scarce literature is available, dispersal limitation seems to be an important factor in determining the spatial population structure in spiders. In this paper, we document on the spatial population structure of the rare wolf spider *Alopecosa fabrilis*, restricted to fragmented grey dunes along the Flemish coast (Belgium) and ask whether its distribution appears to be affected by aspects of patch configuration. Simultaneously, we investigated whether the local distribution of its main parasitoid, the spider wasp *Arachnospila rufa* (Hymenoptera, Pompilidae) was associated with its host. Our results indicate that *A. fabrilis* shows an aggregative population structure, which is determined by the distance to nearest occupied patch, indicating that spatially correlated habitat quality probably determine its occurrence. Although spider wasps are generally characterized as non-specialists, the almost complete covariation between its spatial occurrence and that of *A. fabrilis*, indicates that spider hunting wasps may, at least temporally and locally, show a restricted host-range. As a result, the presence of a rather generalist parasitoid is a good predictor for the presence of nocturnal and burrowing dune wolf spider.

**Keywords:** *Alopecosa fabrilis*, Lycosidae, *Arachnospila rufa*, Pompilidae, metapopulations

In fragmented habitats, species live either in patchy populations or in metapopulations (Harrison 1991; Hanski 1999). In patchy populations, individuals move freely among habitat patches, while in metapopulations, most individuals stay in a single patch during their entire life, but dispersing individuals enhance strong colonization-extinction dynamics. This results in a population structure in which some suitable patches remain vacant. Besides the colonization abilities, changes in habitat quality can also attribute to local extinction dynamics, as demonstrated for specialized butterflies (e.g. Thomas et al. 1992; Ravenscroft 1994; Moilanen & Hanski 1998; Bergman 1999) and backswimmers of the genus *Notopecta* (Briers & Warren 2000). Therefore, studying the spatial structure of populations during successive years by considering aspects of patch geometry, quality and configuration enables us to assess actual dispersal limitation and population dynamics in an indirect way. Snapshots of patch-occupancy incidences provide an alternative indirect meth-

odology to study dispersal abilities or populations viability with respect to population size (patch size) resulting from historical habitat fragmentation and population dynamics. As shown for a coastal dune wolf spider, living in fragmented grassland habitats, patch occupancy patterns may depend both on aspects of habitat quality and on different modes of dispersal through the surrounding matrix (Bonte et al. 2003a). For spiders in general, cursorial dispersal and ballooning induce different colonization and extinction patterns, dependent on the species' mobility, its niche breadth and its propensity for aerial dispersal (Bonte et al. 2003a, 2004b). Especially ballooning dispersal appears to be important for occupancy patterns at extended temporal and spatial scales (Bonte et al. 2003a, 2004a), while cursorial dispersal induces short-term colonization events at small spatial and temporal scales (Bonte et al. 2003a). For spiders, direct estimates of realized dispersal are rare and indicate dispersal distances up to few-hundred meters within suitable habitat (Krei-



ter & Wise 2001; Bonte et al. 2003a; Samu et al. 2003) but restricted dispersal up to few meters in unsuitable, often densely vegetated habitat (Bonte et al. 2003a). Indirect estimates of dispersal, estimated by population genetic analyses, are more common (e.g. Boulton et al. 1998; Ramirez & Fandino 1996; Ramirez & Haakonsen 1999; Gurdebeke et al. 2000). In contrast to the latter, studies on occupancy incidences, ideally conducted during several successive years, reveal indirect estimates of dispersal that are independent of historical bottlenecks and selection pressures in spatially structured habitats (Peterson et al. 2001; Bonte et al. 2003a).

In addition to earlier studies on the mobile wolf spider *Pardosa monticola* (Clerck 1757), we here report on the population structure in coastal dune habitats of the specialized fossorial wolf spider *Alopecosa fabrilis* (Clerck 1757) with limited aerial dispersal abilities (Bonte et al. 2003b) and of its main (winged) parasitoid, *Arachnospila rufa* (Haupt 1927) (Hymenoptera, Pompilidae), knowing to host on larger *Alopecosa* wolf spiders (Koomen & Peeters 1993; Peeters et al. 1994). According to theoretical work, host-parasitoid metapopulations dynamics strongly interfere and occupancy patterns should strongly overlap in case of limited host interpatch dispersal abilities and relatively low infection rates and parasitoid survival rates (Hassel et al. 1991; Comins et al. 1992; White et al. 1996; Hanski 1999).

The population structure of parasitoid and host were investigated in the Flemish coastal dunes, where grey dune habitats, being the optimal habitat for both *A. fabrilis* and *A. rufa*, are truly fragmented since the Second World War (see e.g. Bonte et al. 2003a; Provoost & Bonte 2004). This was done in order to test the following hypotheses: (i) *A. fabrilis* has limited dispersal abilities, resulting in an isolation-dependent population structure, (ii) *A. fabrilis*, having low population densities only occupies larger habitat patches and (iii) local and temporal host-parasitoid association result in similar distribution patterns, although Pompilidae have better dispersal abilities and are believed to be rather generalistic in prey choice according to prey species (Finch 1997). Additionally, as *A. fabrilis* is nocturnal while its parasitoid is diurnally active, we asked whether the presence of a day-active parasitoid

could be an indicator for the presence of populations of a nocturnal, fossorial spider.

## METHODS

**Study Area, Study Species.**—Fieldwork was conducted in the Flemish coastal dunes, located between the cities of De Panne (Belgium) and Bray-Dunes, France (51°05'N, 2°32'E) consisting of 52 discrete grey dune patches, varying between 0.05 and 27.6 ha (Fig. 1). Grey dunes, known as "Fixed coastal dunes" are most readily defined using plant communities. Vegetation includes Atlantic moss dominated dunes (mainly *Tortula ruralis*) as well as dune grassland (with a distinct organic soil layer) belonging to the *Cladonio-Koelerietalia* syntaxon in case of lime rich grey dune, and to the *Trifolio-Festucetalia ovinae* syntaxon in case of decalcified grey dunes (Provoost et al. 2002). In this study, only grey dunes without substantial soil development were surveyed since they are the habitat of both study species (see further). Ecologically it is merely the dry component of the "stressed dune landscape". The main differentiating processes are related to dune fixation, soil formation and vegetation development (Provoost et al. 2002). At present, rough grass and scrub encroachment result in a severe fragmentation within a matrix of dense dune vegetation (shrubs, dense grassland). In an earlier paper, we identified typical spider species for this habitat (Bonte et al. 2002). One of the most habitat-specific species is *Alopecosa fabrilis*, although its overall Indicator Value was low, hence, indicating a relative low occupancy rate.

*Alopecosa fabrilis* is used as model organism in this study. It is the largest lycosid species, living in self-made burrows in dry sandy habitats from temperate regions in Europe (males: 10–12 mm; females: 13–16 mm; Roberts 1998). The species has a nocturnal life style in which especially males leave their burrow in search for mating partners during autumn, with a peak activity during September (Roberts 1998; Bonte, unpub. data.). Females are active during autumn, but especially during late winter and early spring. The species occurs in low densities, has a biannual life cycle (Bonte et al. unpub. data) and does not perform ballooning dispersal under laboratory conditions (Bonte et al. 2003b).

During its period of activity, the spider



Figure 1.—Map of the surveyed grey dune habitat patches in the coastal dunes of De Panne-Bray Dunes, Belgium. Black: patches occupied by *Alopecosa fabrilis*; white: unoccupied patches. Circles indicate patches not occupied by *Arachnospila rufa*.

hunting wasp (Hymenoptera, Pompilidae) *Arachnospila rufa* has been observed to be the main predator (Koomen & Peeters 1993; Peeters et al. 2004; Bonte, pers. obs.; Nieuwenhuijsen, pers. comm.). *Alopecosa schmidtii* (Hahn 1834) has been recorded as prey in Middle-Europe (Schljachtenok 1996). Female pompilids provide each cell of their nest below the sand surface with only a single paralyzed spider, on which one egg is laid. *Arachnospila rufa* is large (body size up to 18 mm) and common in sandy regions of Belgium and the Netherlands. It reaches adulthood from June–October (Peeters et al. 2004; Nieuwenhuijsen in press). More detailed information about its ecology and life history is unfortunately not available. Voucher specimens of both *Alopecosa fabrilis* and *Arachnospila rufa* are deposited at the Royal Belgian Institute for Natural Sciences.

**Field Survey & Statistical Analyses.**—Occupancy patterns of *A. fabrilis* were recorded from 25 August–7 October 2003 using pitfall traps (diameter 9 cm, 6% formaldehyde-de-

tergent solution). In each of the 52 grey dune patches, at least five traps were randomly placed, depending on the patch area. Patches were digitized from aerial orthophotographs with a Geographic Information System (Arcview 3.1) and discrimination of vegetation types was based on vegetation-specific red (RED) and near-infrared (NIR) reflectance values (Provoost et al. 2002). Because of its high activity during this season, the use of pitfall traps have been shown to be very useful in catching this typical spider species living within this habitat (Bonte et al. 2004c). The presence of the hunting wasp was recorded in the same pitfall traps, but completed with detailed field surveys during sunny days. Although not all observed specimens were collected to confirm identification, individuals could be identified in the field by their large size and distinct abdominal coloration. From GIS, we measured patch area, the distances to the nearest suitable patch, as a measure of patch isolation and distance to the nearest occupied patch (nearest-neighbor distance) as



measurement of population isolation. For *A. rufa*, we did not use the latter isolation measurement because its presence was only recorded during September, hence ignoring possible different distribution patterns during the previous summer-period.

Patch occupancy patterns for *A. fabrilis* (0: vacant; 1: occupied) were analyzed by logistic models for binomial data and logit-link with backward elimination of the non-significant parameters (SAS 9.2). Patch area, patch isolation and the interaction between both were included as independent variables. For *A. rufa*, the occupancy status of the patch by *A. fabrilis* was used as an additional categorical variable.

## RESULTS

Patch occupancy of *Alopecosa fabrilis* was not significantly influenced by patch area ( $\chi^2_1 = 2.255$ ;  $P = 0.133$ ). The distance to the nearest suitable habitat ( $\chi^2_1 = 1.168$ ;  $P = 0.280$ ) and the interaction between both ( $\chi^2_1 = 0.208$ ;  $P = 0.648$ ) did not contribute significantly. If the nearest-neighbor distance was taken into account, a significant negative relationship was found between isolation and patch occupation (estimated slope:  $-0.035 \pm 0.014$ ;  $\chi^2_1 = 6.322$ ;  $P = 0.012$ ; Fig. 2). Other parameters remained non-significant. Although the model describes patch occupancy patterns in a significant way, 32.7% of the cases were misclassified. Mainly patches near the inner dune front were occupied (Fig. 1). If only patches at the inner dune front were used for analysis, neither distance to the nearest patch ( $\chi^2_1 = 0.028$ ;  $P = 0.865$ ), distance to the nearest occupied patch ( $\chi^2_1 = 1.144$ ;  $P = 0.285$ ) or area ( $\chi^2_1 = 0.476$ ;  $P = 0.490$ ) explained distribution patterns.

After backward elimination of non-significant parameters, the occupancy of *Arachnospila rufa* was only determined by the presence of *Alopecosa fabrilis* ( $\chi^2_1 = 34.41$ ;  $P < 0.0001$ ). No other lycosid species were recorded during the survey period. Landscape geometry appears to be unimportant during this season since the explanatory power of both patch area and patch isolation are extremely low (all variables and interactions:  $\chi^2 < 1.29$ ;  $P > 0.256$ ). Patches occupied by *A. fabrilis* but not by *A. rufa* ( $n = 4$ ) during this period were significantly smaller than those ( $n = 11$ ) occupied by both species (Mann-Whit-

ney U-test:  $Z = 2.74$ ;  $P = 0.006$ ; Fig. 2). *Arachnospila rufa* was not recorded in patches without *A. fabrilis* populations.

## DISCUSSION

**Population structure of *Alopecosa fabrilis*.**—Our results demonstrate that the distance to the nearest occupied patch contributed significantly to the patch-occupancy model, whereas the overall habitat structure (i.e. geometry and configuration of all available patches) did not. As a result, the population structure seems not to be affected by local potential population sizes (related to local population viability; Hanski 1999) and distant dispersal abilities by ballooning. The latter is in agreement with the absence of aerial dispersal under laboratory conditions (Bonte et al. 2003b). As only the nearest-neighbor distance contributed significantly to the patch-occupancy model, the population structure of *A. fabrilis* seems to be clearly aggregative, indicating low abilities to disperse (and penetrate) cursorially through the hostile matrix or a predominant role of habitat quality. Our data, however, only result from a short term survey. But preliminary data on patch occupancy patterns from 2004 show similar distribution patterns (Bonte et al. unpub. results), indicating the absence of strong turn-over dynamics at extended, though still rather short time spans. The fact that patch area (related to local population size) does not explain occupancy patterns seems to indicate that the spatial population structure is more likely to be determined by random extinction-colonization dynamics within aggregative clusters of closely connected suitable habitat remnants, which appear to be situated near the inner dune front. As the interaction between patch size and patch isolation does not explain occupancy patterns, a rescue effect resulting from source-sink dynamics is unlikely (Dias & Blondel 1996).

The aggregated pattern may result from dispersal limitation after historical population dynamics or from spatially correlated habitat characteristics, related to habitat quality, as experienced by the species. Although both are possible, the second seems to be more probable as especially patches near the inner dune front were occupied. In coastal dunes, characterized by a successive ontogenesis, grey dunes, although structurally similar may show

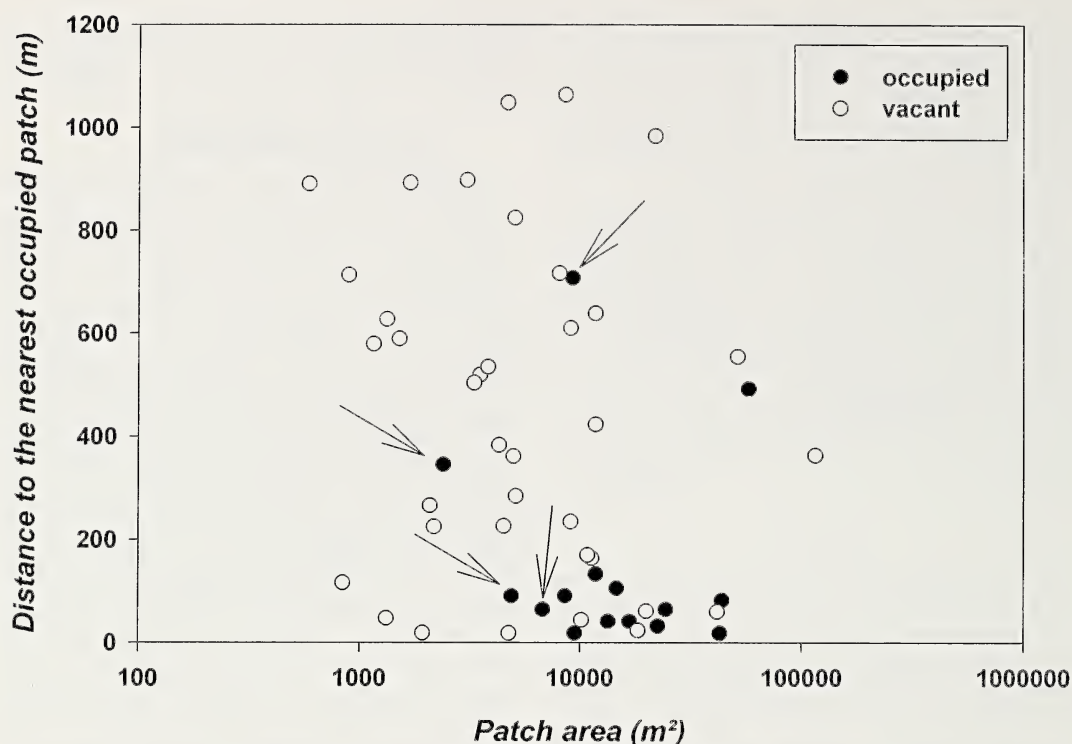


Figure 2.—Relation between patch area, nearest-neighbor distance and occupancy incidence for *A. fabrilis* populations. Arrows indicate patches occupied by *A. fabrilis*, but not by its predator *A. rufa*.

extensive spatial correlation in environmental characteristics related to microclimate, soil properties and aeolic dynamics (sand overblowing). The fact that considerable non-spatial correlated variation in habitat quality affects spatial structural patterns has already been demonstrated by e.g. Briers & Warren (2000) and Bonte et al. (2003a). For a fossorial species like *A. fabrilis*, it is not impossible that e.g., grain size properties, soil water retention, soil formation and the intensity of sand overblowing strongly determine burrowing ability and the sustainability of created burrows. In the same coastal dune landscape, the grassland inhabiting wolf spider *P. monticola* shows a habitat-quality dependent population structure in which both patch area and patch connectivity determined occupancy patterns (Bonte et al. 2003a), although not in an aggregative way. As vegetation structure is alike in all investigated grey dune patches, similarity in habitat quality for *A. fabrilis* is probably more related to pedological (possibly soil stability or differences in grain size near the inner dune front) or microclimatological (less buffered temperatures far from the sea)

conditions and, possibly, the reason for the observed clustered occurrence. Also, the absence of *A. fabrilis* in large patches more close to the sea, in which large populations should be able to persist, provides more likely evidence for a reaction towards spatially correlated environmental properties and optimal habitat quality in older grey dunes, situated near the inner dune front. In this case, dispersal limitation is of inferior importance, as illustrated by the model in which only patches near the inner dune front were included.

**Host-parasitoid association.**—Spatially explicit host-parasitoid metapopulation models generate spatially correlated abundance and, hence, occupancy patterns in host and parasitoid (Hanski, 1999). *Arachnopsila rufa* and related spider hunting wasps, however, appear to be more generalist parasitoids on (larger) lycosid species (Koomen & Peeters 1993; Endo & Endo 1994; Finch 1997; Peeters et al. 2004). The almost complete match between occupancy incidences of host and parasitoid indicate that, at least in the Flemish coastal dunes and during the survey period, *A. rufa* behaves as a specialized parasitoid on *A.*



*fabrilis*. This indicates that at least one species of pompilid wasp may behave as a host-specialist during some periods of its adult life. According to White et al. (1996), spatial population patterns in which both host and parasitoid occur in the same patches are only static in case of low host dispersal and low parasitoid survival. Certainly the first assumption seems to be fulfilled in our study. However, *A. rufa* is already adult earlier in the season, and should, as a result, behave more flexibly in prey selection. As predicted by optimal foraging theory, prey size selection should be optimized in relation to the species' load-carrying capacity (Evans 1962; Coelho & Ladage 1999). The latter authors indeed found that large female wasps searched for prey that matched their own body mass and lift capacity. As a result, *A. rufa* should prey on similarly large-bodied lycosid species or show behavioural flexibility according to the available prey spectrum. Taking into account the need for sandy habitats for prey burrowing, *A. rufa* seems to be restricted to dynamic dune habitats in which soil development is poor and bare sand sufficiently available. Female *A. fabrilis* disappear from the population in late winter and early spring and are not available as host during the early beginning of the hunter wasp's adulthood (Bonte, unpub. data). Other large-bodied lycosid species, occurring in these habitats include only *Alopecosa cuneata* (Clerck 1757) and *A. barbipes* (Sundevall 1833) (Bonte et al. 2002), also having a spring activity, and are as a result neither available during summer. Possibly, *A. rufa* uses smaller lycosids as host during early summer (*Arctosa perita* (Latreille 1799) or subadult *A. fabrilis*), potentially resulting in different spatial distribution patterns.

The fact that *A. rufa* was only absent from small patches, inhabited by *A. fabrilis* seems to provide evidence that higher trophic levels require larger habitats (Holt 1996; Holt et al. 1999), but may also be an artifact in our sampling strategy if smaller patches are only accidentally visited by the spider wasp, hence reducing encounter chances in the field. According to Holt (1999), higher trophic ranks need larger areas if dispersal is limited, have closed populations and show a high degree of specialization towards resource species. Certainly the latter seems to hold for the (at least temporal and local) *A. rufa*-*A. fabrilis* asso-

ciation. Assuming that our findings are not due to sampling artifacts, parasitoid absence in small populations indicates low dispersal abilities or at least low dispersal motivation in spider wasp within spatially structured suitable habitat surrounded by hostile matrix vegetation.

Also, since both juvenile and adult *A. fabrilis* stay in their burrow during day, prey selection by *A. rufa* has probably to rely on olfactory and not on visual cues because burrow entrances are not visible, as also observed in spider hunting wasps preying on day-active wolf spiders (e.g., *Pompilus cinereus* (Fabricius 1775); Bonte pers. obs.) and in sphecoid wasps (although only at short distance after visual detection; Anton & Gnatzy 1998).

In fragmented coastal dune habitats, host and parasitoid show, at least temporally and locally, a similar aggregative spatial population structure, indicating the importance of (lack of) dispersal and possibly spatially correlated habitat characteristics in structuring patch occupancy patterns. Additionally, the spider hunting wasp *A. rufa* appears to behave as a specialized parasitoid during the main activity period of its optimal prey with restricted dispersal motivation. During this period, the presence of an assumed generalist parasitoid is a good predictor for the presence of nocturnal and burrowing dune wolf spider in larger habitat patches in the Flemish coastal dunes.

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## EARLY SUCCESSION OF A BOREAL SPIDER COMMUNITY AFTER FOREST FIRE

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**ABSTRACT.** Ground-living spiders were studied, using pitfall traps, 3–4 months after a wildfire, and then during three post-fire summers. The study area was a pine (*Pinus sylvestris*) forest in southwestern Finland. Lycosidae dominated in individual numbers at the burned site and Linyphiidae at the control. In species numbers, Linyphiidae dominated at both sites, and Lycosidae, Gnaphosidae and Theridiidae were more species-rich at the burned than control site. The lycosid *Xerolycosa nemoralis* was dominant at the burned site, and the linyphiid *Agyneta cauta* at the control. Abundant species found only at the burned site included *Xerolycosa nemoralis*, *Pardosa riparia*, *Acantholycosa lignaria* and *Micaria silesiaca*. *Tapinocyba pallens* and *Pardosa lugubris* occurred at both sites in large numbers. A slight positive effect of fire on the species richness was found. Species with more or less stable abundance at the burned site during the study period included *Pardosa riparia*, *P. lugubris* and *Diplostyla concolor*. Increasing abundance in successive years occurred for *Acantholycosa lignaria*, *Micaria silesiaca*, *Xerolycosa nemoralis* and for the family Lycosidae. *Euryopis flavomaculata*, *Agyneta rurestris*, *Tapinocyba pallens* and the family Linyphiidae showed a decreasing abundance during the study years. The spider community at the burned site remained clearly different compared to the control during three post-fire summers, primarily caused by the abundance of Gnaphosidae and Lycosidae.

**Keywords:** Araneae, ground-living spiders, post-fire succession, pine forest, Finland

Intensive and regular fires are a natural part of the ecology in many areas and have an effect on the fauna in those habitats. This is well-known in the Mediterranean-type of ecosystems (e.g., Stamou 1998; Moretti et al. 2004). But in the boreal taiga forest zone of the Holarctic, fires occur normally at long intervals, and the fauna living there is less adapted to the fires.

Forest fires are rare and small in Finland, mainly due to active fire control. The situation contrasts clearly with that in the boreal coniferous forest zone both in Russia and Canada where extensive areas of forest are yearly destroyed by fire (e.g., Koponen 1993). Therefore, little information is available on the effects of forest fire on spiders and their post-fire succession in Finland or in the whole of Fennoscandia. In Finland, Huhta (1971) studied succession after prescribed burning, and Koponen (1988, 1989, 1995) studied the effects of natural fire in a subarctic birch woodland in Finnish Lapland. Some data on the first post-fire summer at the present study site have been given by Koponen (2004). Hauge & Kvamme (1983) studied spiders from forest fire areas in Norway. In the pre-

sent paper, the post-fire succession of ground-living spiders in a boreal forest in southwestern Finland is explored.

### METHODS

The study area is situated in Tammela, Riihivalkama, east of the Torronsuo National Park (Finnish Grid 27°E: 6740:323); ca. 60°44'N, 23°45'E. The study site is a dry gentle slope with young pine (*Pinus sylvestris*) trees, diameter 20 cm or less.

The forest (about 150 hectares) was burned on 9–10 June 1997. It was totally burned: all moss and lichen as well as vascular plant vegetation was destroyed. The dead pines were still standing there in autumn 1997, but they were cut down and removed in May 1998. Under the 2–5 mm thick layer of ash and charcoal there was a humus layer, but locally only mineral soil. The black and open site was sunny, dry and warm, especially during the first post-fire year. The distance from non-burned forests to the study site was at least 150 m.

Ground living spiders were studied 3–4 months after the fire, in order to find colonizers or species which had survived the fire. Twenty-four pitfall traps with ethylene glycol



Table 1.—Ground and field layer vegetation around the traps at burned and control sites in Tammela, Finland. New plant species appearing at different stages of the succession are indicated by +.

Burned site	Coverage %	Plant species
1997 September	<1%	—
1998 May	<1%	—
July	10%	<i>Epilobium angustifolium</i> , <i>Ceratodon</i> moss
September	20%	
1999 May	30%	+ <i>Luzula</i> + <i>Calluna vulgaris</i>
July	50%	
September	55%	
2000 May	60%	+ <i>Deschampsia</i>
August	80%	+ <i>Rubus idaeus</i>
Control site	100%	<i>Pleurozium</i> and <i>Dicranum</i> moss, <i>Linnaea borealis</i> , <i>Trientalis eu-</i> <i>ropea</i> , <i>Vaccinium vitis-idaea</i> , <i>V. myrtillus</i> etc, and <i>Pinus syl-</i> <i>vestris</i>

and detergent (mouth diameter 60 mm, with covers) were placed there from 12 September–17 October 1997. During the following three summers, 10 similar traps were placed in the burned site and 10 in a control site about 300 m from the fire. Coverage of the ground and field layer vegetation was estimated visually around the traps (Table 1). There is no information available of the previous fire history of the study area. The climatic conditions varied during the study years; the summer 1998 was cool and rainy, 1999 was warm, and 2000 near the average.

The yearly study periods were: 9 May–27 September 1998; 15 May–28 September 1999; 14 May–10 August 2000. We removed the traps in August 2000 due to interference by people visiting the site. The spider material, deposited on the Zoological Museum, University of Turku, consisted of about 1100 identifiable specimens from the burned and 1540 from the control site. Nomenclature is mainly after Platnick (2004), except *Agyneta/Meioneta*.

RESULTS

Altogether 91 species of ground-living spiders were found, 70 at the burned site and 59 at the unburned control site. The family Linyphiidae clearly dominated in species numbers.

**Post-fire autumn.**—The spiders were trapped 3–4 months after the fire in autumn 1997. Altogether, 16 species were found during this short, autumnal collecting period. *Tapinocyba pallens* (O.P.-Cambridge 1872) clearly dominated (25.0%), and *Tenuiphantes*

*mengei* (Kulczynski 1887) (13.6%) and *Agyneta rurestris* (C.L. Koch 1836) (11.4%) were also abundant. *Agroeca proxima* (O.P.-Cambridge 1871), *Pardosa lugubris* (Walckenaer 1802), *Trochosa terricola* Thorell 1856, *Porhomma pallidum* Jackson 1913, *Gnaphosa bicolor* (Hahn 1833) and *Haplodrassus signifer* (C.L. Koch 1839) were represented by at least two specimens. Linyphiids were the dominant spider family in terms of individuals (Table 2) and half of the species caught were linyphiids. For a more detailed description of the results from the autumn 1997, see Koponen (2004).

**Following summers.**—The general composition of the spider assemblages at the burned and control sites is shown in Table 2. Linyphiids dominated in the number of species, at both the control site as well as at the burned site, during the study years. Species numbers of Lycosidae, Gnaphosidae and Theridiidae were higher at the burned than the control site. Faunal similarity, as percentage of species found at both sites, in 1998, 1999 and 2000 was 28%, 35% and 25% respectively. The situation in 2000 was somewhat biased by the destroyed traps at the burned site (see above). There were no great differences in the yearly species richness between the sites; however, during the 1998 and 1999 summers, more species were found at the burned site: 39 vs. 35 and 51 vs. 46 respectively (Table 2).

The family Linyphiidae was dominant in individual numbers at the control site (69.6–86.7%) during the whole study period, and

Table 2.—Family composition of individuals (%) and species (no. of species) of the spider fauna at the burned (bu) and control (co) sites, 1997–2000. Trapping periods: 12 September–17 October 1997, 9 May–27 September 1998, 15 May–28 September 1999, 14 May–10 August 2000.

	1997	1998		1999		2000	
	bu	bu	co	bu	co	bu	co
Individuals							
Linyphiidae	75.4	59.4	86.7	29.0	82.9	15.9	69.6
Lycosidae	10.8	32.5	2.3	64.8	8.5	62.0	18.7
Gnaphosidae	6.2	2.2	1.1	3.1	0.7	20.9	3.0
Theridiidae	1.5	4.3	1.4	2.1	1.4	0.9	0.4
Others	6.2	1.6	8.5	1.0	6.5	0.3	8.3
Species							
Linyphiidae	8	21	22	22	29	9	24
Lycosidae	3	7	2	8	4	6	3
Gnaphosidae	2	4	2	7	2	6	4
Theridiidae	1	3	1	4	1	4	2
Others	2	4	8	10	10	5	12
Total	16	39	35	51	46	30	45

also at the burned site during early succession (1997–98) while Lycosidae dominated at the burned site during the two following summers (1999–2000: 62.0–64.8%) (Table 2). No trend was found in catches (#individuals/trap/day) between the sites; in 1998 and 2000 more specimens were caught at the burned and in 1999 at the control site (Table 2).

The most abundant species at both sites, 1998–2000, are shown in Tables 3–4. The lycosid *Xerolycosa nemoralis* (Westring 1861) was the dominant species at the burned site during the whole period (Table 3). *Pardosa riparia* (C.L. Koch 1833), *P. lugubris* and *Alopecosa pulverulenta* (Clerck 1957) (Lycosidae), and *Diplostyla concolor* (Wider 1834) (Linyphiidae) were also abundant, 1998–2000. *Euryopis flavomaculata* (C.L. Koch 1836) and *Agyneta rurestris* were abundant during the first post-fire summer (1998) but later they were less numerous. *Tapinocyba pallens* had a similar but less clear trend. On the other hand, *Micaria silesiaca* L. Koch 1875 and *Acantholycosa lignaria* (Clerck 1757) were trapped in good numbers during the latter summers (1999–2000).

At the control site, the composition of abundant linyphiid species was rather stable during the study years (1998–2000), see Table 4. In contrast to the burned site with lycosids dominating, here linyphiids were most numerous. They were represented primarily by

the species *Agyneta cauta* (O.P.-Cambridge 1902), *Tapinocyba pallens*, *Centromerus arcanus* (O.P.-Cambridge 1873) and *Agyneta conigera* (O.P.-Cambridge 1873). These were followed, based on total abundance, by the lycosids *Pardosa lugubris*, which was, however, caught in low numbers during the first summer, and *Alopecosa aculeata* (Clerck 1757). Typical species at the control site were also the linyphiids *Diplocentria bidentata* (Emerton 1882), *Walckenaeria antica* (Wider 1834), *W. cucullata* (C.L. Koch 1836), *Minyriolus pusillus* (Wider 1834), *Tenuiphantes alacris* (Blackwall 1853), *T. tenebricola* (Wider 1834), and *Bathyphantes parvulus* (Westring 1851). From other families, *Zora nemoralis* (Blackwall 1861), *Z. spinimana* (Sundevall 1833), *Haplodrassus soerenseni* (Strand 1900) and *Cryphoea silvicola* (C.L. Koch 1834) can be mentioned.

Abundant species found only at the burned site included *Xerolycosa nemoralis*, *Pardosa riparia*, *Acantholycosa lignaria*, *Micaria silesiaca*, *Phrurolithus festivus* (C.L. Koch 1835) and *Agyneta rurestris*; and *Tapinocyba pallens* and *Pardosa lugubris* were found at both sites. Faunistically interesting species at the burned site included *Agyneta gulosa* (L. Koch 1869) (a northern species in Finland), and *Troxochrota scabra* Kulczynski 1894 and *Troxochrus nasutus* Schenkel 1925 (rare, mainly southern species).



Table 3.—The most abundant spiders trapped at the burned site, 1998–2000. Number of individuals (n), percentage and rank (only for the 10 most abundant in each year) are given.

	1998			1999			2000		
	n	%	Rank	n	%	Rank	n	%	Rank
<i>Xerolycosa nemoralis</i>	29	11.9	(1)	92	20.4	(1)	103	36.8	(1)
<i>Tapinocyba pallens</i>	27	11.2	(2)	36	8.0	(4)	2	0.5	
<i>Alopecosa pulverulenta</i>	25	10.3	(3)	36	8.0	(4)	4	1.1	(10)
<i>Pardosa riparia</i>	24	9.9	(4)	71	15.8	(2)	34	12.1	(2)
<i>Euryopis flavomaculata</i>	21	8.7	(5)	8	1.8		1	0.3	
<i>Agyneta rurestris</i>	16	6.6	(6)	9	2.0	(10)	3	0.8	
<i>Pardosa lugubris</i>	15	6.2	(7)	21	4.7	(6)	19	6.8	(4)
<i>Centromerus arcanus</i>	9	3.7	(8)	2	0.4		—		
<i>Diplostyla concolor</i>	8	3.3	(9)	42	9.3	(3)	10	3.6	(6)
<i>Tenuiphantes mengei</i>	7	2.9	(10)	10	2.2	(9)	—		
<i>Micaria silesiaca</i>	—			11	2.4	(7)	26	9.3	(3)
<i>Walckenaeria antica</i>	2	0.8		11	2.4	(7)	9	2.4	(7)
<i>Acantholycosa lignaria</i>	—			4	0.9		18	6.4	(5)
<i>Gnaphosa bicolor</i>	2	0.8		1	0.2		8	2.1	(8)
<i>Phrurolithus festivus</i>	—			2	0.4		7	1.9	(9)

DISCUSSION

The number of species caught 3–4 months after the fire was rather high, although the trapping period was short (see also Koponen 2004). This can, at least partly, be a result of the number of traps in 1997 (24 vs. 10 in following summers). Whether some of the species had survived the fire is unknown. Some stationary invertebrates (gastropods, millipedes, female coccids) were also caught in the traps during the autumn of 1997. These seem to have survived under large stones or in the soil (see also Punttila et al. 1994), the same may be true for some spiders. On the other hand, silk lines were seen in great numbers on the burned ground indicating ballooning.

Pioneer species at the burned site are *Agyneta* species (subgenus *Meioneta*), e.g. *A. rurestris*, which was caught in highest numbers among the pioneer species, as well as *Erigone atra* Blackwall 1833 and *Oedothorax retusus* (Westring 1851) (cf. Merrett 1976; Winter et al. 1983; Koponen & Niemelä 1994). None of them was found at the control site.

The dominant species at the burned site, *Xerolycosa nemoralis*, has been found in Finland as a colonizer of open, dry and warm areas, often human-influenced. These areas include dried peat bogs (Koponen 1979) and heavily polluted areas (Koponen & Niemelä 1994). In a study of burned pine forests in northern Germany, Schaefer (1980) found *X.*

*nemoralis* in high numbers in young pine plantations but not at the burned sites, where *Pardosa lugubris* dominated among lycosids. *Pardosa lugubris* was one of the most abundant species both at the burned and control site in Tammela.

*Pardosa riparia*, *Acantholycosa lignaria*, *Micaria silesiaca* and *Phrurolithus festivus*, species found only at the burned site, have often been caught in open areas (e.g., Hänggi et al. 1995; Marusik et al. 2004). Species preferring open and warm areas, like many lycosids, have often been caught in high numbers at burned localities (Brabetz 1978; Schaefer 1980; Koponen 1993, 2004; Buddle et al. 2000). Niwa & Peck (2002) studied the influence of prescribed fire on spiders in conifer stands in Oregon and found, in agreement with the present study, that Lycosidae and Gnaphosidae were more numerous at burned and Linyphiidae at unburned sites.

A slight positive effect of fire on the species richness could be seen (cf. also Moretti et al. 2004). The species-rich fauna at the burned site was a combination of pioneer species (e.g., *Agyneta rurestris*, *Oedothorax retusus*), of thermophilous (*Xerolycosa nemoralis*, *Micaria silesiaca*) and eurytopic (*Diplostyla concolor*) species often preferring open sites, and of some typical pine forest species (*Tapinocyba pallens*, *Centromerus arcanus*). On the other hand, both species and individual

Table 4.—The most abundant spiders trapped at the control site, 1998–2000. Number of individuals (n), percentage and rank (only for the 10 most abundant in each year) are given.

	1998			1999			2000		
	n	%	Rank	n	%	Rank	n	%	Rank
<i>Centromerus arcanus</i>	44	16.1	(1)	70	8.8	(4)	21	5.6	(6)
<i>Tapinocyba pallens</i>	43	15.8	(2)	77	9.7	(3)	22	5.9	(5)
<i>Agyneta cauta</i>	20	7.3	(3)	158	20.0	(1)	56	14.9	(1)
<i>A. conigera</i>	17	6.2	(4)	86	10.9	(2)	24	6.4	(4)
<i>Diplocentria bidentata</i>	13	4.8	(5)	10	1.3		11	2.3	(8)
<i>Walckenaeria antica</i>	13	4.8	(5)	18	2.3		6	1.3	
<i>Diplostyla concolor</i>	11	4.0	(7)	20	2.5	(7)	8	1.7	(10)
<i>Zora nemoralis</i>	11	4.0	(7)	4	0.5		2	0.4	
<i>Bathypantes parvulus</i>	9	3.3	(9)	9	1.1		1	0.2	
<i>Tenuiphantes tenebricola</i>	9	3.3	(9)	18	2.3		6	1.3	
<i>Pardosa lugubris</i>	4	1.5		44	5.6	(5)	51	13.6	(2)
<i>Alopecosa aculeata</i>	8	2.9		15	1.9		29	7.7	(3)
<i>Minyriolus pusillus</i>	7	3.6		30	3.8	(6)	8	1.7	(10)
<i>Walckenaeria cucullata</i>	8	2.6		19	2.4	(8)	8	1.7	(10)
<i>Tenuiphantes alacris</i>	5	1.8		19	2.4	(8)	6	1.3	
<i>Cryphoea silvicola</i>	5	1.8		19	2.4	(8)	4	0.8	
<i>Zora spinimana</i>	1	0.4		—			12	2.5	(7)
<i>Haplodrassus soerenseni</i>	2	0.7		5	0.6		11	2.3	(8)

numbers outside of the four main families (Linyphiidae, Lycosidae, Gnaphosidae and Theridiidae) were higher at the control than at the burned site (see Table 2), indicating a generally more diverse fauna in the unburned forest.

Some general trends in the spider assemblage at the burned site could be found during the study years. Species with more or less stable abundance at the burned site include *Pardosa riparia*, *P. lugubris* and *Diplostyla concolor*. Increasing abundance in successive years was true for *Acantholycosa lignaria*, *Micaria silesiaca*, *Xerolycosa nemoralis* and for the family Lycosidae. On the other hand, *Euryopis flavomaculata*, *Agyneta rurestris*, *Tapinocyba pallens* and the whole Linyphiidae showed decreasing numbers during the study years. The spider community at the burned site remained clearly different compared with the control during the study period's three post-fire summers. This was primarily caused by the species diversity and abundance of Gnaphosidae and Lycosidae.

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## ARE SALT MARSH INVASIONS BY THE GRASS *ELYMUS ATHERICUS* A THREAT FOR TWO DOMINANT HALOPHILIC WOLF SPIDERS?

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**ABSTRACT.** As a result of the *Elymus athericus* (Poaceae) invasion in the last ten years, a major change in vegetation cover has occurred in salt marshes of the Mont Saint-Michel bay (France). In this study, we investigated if the high conservation value of invaded salt marshes is preserved. Abundances, densities and flood resistance abilities of the dominant halophilic species *Arctosa fulvolineata* (nocturnal lycosid) and *Pardosa purbeckensis* (diurnal lycosid) were compared in both natural and invaded habitats. *Elymus* invasion involved both positive and negative aspects with respect to the conservation value of the salt marshes invaded: the *P. purbeckensis* population was clearly reduced in invaded habitats, whereas *A. fulvolineata* seemed to derive high benefits from the invasion. We supposed that abiotic parameters of the new habitat (mainly vegetation and litter characteristics) affected the two species differently with respect to their aut-ecology and their flood resistance abilities. Furthermore, food resources (estimated by different macrofauna density measurements) were likely to be reduced for *P. purbeckensis* in invaded habitats and unchanged for *A. fulvolineata*. Lastly, we hypothesize that individuals of *P. purbeckensis* are subject to increased interspecific competition (measured as intra-guild densities), whereas spiders from the same guild as *A. fulvolineata* have not increased in invaded habitats, resulting in an unchanged competition level.

**Keywords:** Conservation value, halophilic species, habitat change, invasive species, food resources

Salt marshes are one of the rarest ecosystems in the world (Lefeuvre et al. 2000), with a linear but fragmented distribution along coasts, therefore representing a high interest in terms of nature conservation (e.g., Gibbs 2000; Bakker et al. 2002). In fact, these ecosystems host a poorly diversified flora and fauna, which possess a low number of species that are threatened directly or indirectly by human activities such as habitat destruction, diffuse soil pollution from adjacent cultivated fields, and overgrazing (Desender & Maelfait 1999; Adam 2002). The high conservation value of these habitats is also due to the high specificity of its fauna, adapted to two main abiotic factors, high soil salinity and regular submergence by seawater. Due to tidal events, natural salt marshes present a specific plant cover (spatial succession from the high to the low marsh) and specific invertebrate commu-

nities dominated by some “halophilic arthropods” (Foster & Treherne 1976; Irmiler et al. 2002; Pétilion et al. 2004).

In the Mont Saint-Michel bay, France, salt marshes have been invaded by a native species *Elymus athericus* (Link) Kerguelen (Valéry et al. 2004). This high marsh-living grass (Poaceae) started to invade the salt marsh 10 years ago (Bouchard et al. 1995) and now covers some marshes to the mean sea tide level. This progression is characteristic of an invasive species that is common in European salt marshes (Bockelmann & Neuhaus 1999). Nevertheless, the effects of *E. athericus* invasions on the high conservation value of salt marshes remain unknown. Spiders constitute an abundant, diversified and well-known taxonomic group in salt marshes (Fouillet 1986; Desender & Maelfait 1999), including specialist (stenotopic) species, the so-called “hal-



Table 1.—Synthesis of field experiments carried out in the Mont Saint-Michel bay salt marshes (‘Ferme Foucault’ and ‘Vivier-sur-mer’ sites).

Parameter	Methodology	Period	Number of replicates
Target species abundances	Pitfall trap (r = 5 cm)	April–November 2002	8
Target species densities	Depletion quadrat (1 m <sup>2</sup> )	June–July 2003	32
Target species abundances before and after the tide	Pitfall trap (r = 5 cm)	April 2004	12
Abiotic parameters	WET sensor and manual measurements	July–August 2002	16
Macrofauna densities	Soil cores (r = 5 cm)	October 2003	6
Amphipod densities	Depletion quadrats (1 m <sup>2</sup> )	June 2003	4
Total spider densities	Depletion quadrats (0.25 m <sup>2</sup> )	June 2002	16

ophilic species” (Hänggi et al. 1995) or “salt marsh resident species” (Pétillon et al. 2004). In Europe, the numerically dominant hunting spiders in salt marsh ecosystems are the rare lycosid species *Pardosa purbeckensis* F.O. Pickard-Cambridge 1895 and *Arctosa fulvolineata* (Lucas 1846) (Fouillet 1986; Baert & Maelfait 1999; Elkaim & Rybarczyk 2000). *Pardosa purbeckensis* will be considered in this study as different from *P. agrestis*, dominant in Central Europe agricultural landscapes (e.g., Samu & Szinetár 2002) and inland salt marshes (e.g., Zulka et al. 1997), mainly because of its morphological characteristics (as described in Locket & Millidge 1951) and its osmoregulatory abilities (Heydemann 1970). *Arctosa fulvolineata* is classified as a nationally endangered species in the United Kingdom (Harvey et al. 2002) and belongs to the “rare species” category in the Ramsar Convention.

The aim of the study was to investigate if the newly created vegetation cover induced by the invasion of *Elymus athericus* still constitutes a suitable habitat for these two species of high conservation value. To explain the potential impact of the invasive plant on spider species habitat preferences, natural and invaded habitats were characterized by abiotic and biotic components. We hypothesized that *Elymus athericus* changed the general microhabitat characteristics and induced 1) an effect on species density, activity density and flooding resistance due to less appropriate abiotic parameters (e.g., salinity or litter depth), 2) a change in the quality and quantity of food resources, and 3) a variation in the predation rate (measured as intra-guild densities) upon

the two species *Arctosa fulvolineata* and *Pardosa purbeckensis*.

METHODS

**Study sites and field surveys.**—The Mont Saint-Michel bay, located between Brittany and Normandy (North West France), is unique in Europe for its tidal amplitude, which reaches 15 meters (the second largest in the world). This exceptional phenomenon results in the extension of salt marshes and mud flats, which together cover 250 km<sup>2</sup>. Salt marshes are only submerged during spring tides (i.e. monthly strong tides) and are then inundated during two hours per tide (Lefeuvre et al. 2000). The uppermost parts of the salt-marshes are delimited by dikes and are not submerged during high tides.

Natural stations (dominated by *Atriplex portulacoides*, Chenopodiaceae) and invaded stations (dominated by *Elymus athericus*, Poaceae) were located at the same distance from the dike. Habitat characterization and measurements of spider activity and density were carried out at four stations (two natural and two invaded) located at the ‘Ferme Foucault’ site’ (Normandy, 48°55’N, 1°52’W) whereas experiments on species reactions to flooding were carried out at six stations (three natural and three invaded) located at the ‘Vivier-sur-mer’ site (Brittany, 48°60’N, 1°78’W).

**Spider sampling.**—*Spider abundances:* Spiders were sampled with pitfall traps, consisting of polypropylene cups (10 cm diameter, 17 cm deep) set into the ground so that the lips were flush with the soil surface. Ethylene glycol was used as preservative, because of its lack of effects on spider catches

Table 2.—Mean spider activity abundances (number of individuals/day/meter  $\times 10$ ) and mean densities (number of individuals/m<sup>2</sup>) in invaded and natural vegetations, and statistical comparisons using ANOVA (Code: n.s. = non significant, \* =  $P < 0.05$ , \*\* =  $P < 0.01$ ).

	Natural plots	Invaded plots	F-ratio	Code
Spider abundances				
<i>Arctosa fulvolineata</i>	9.31 $\pm$ 3.09	9.83 $\pm$ 3.15	0.01	n.s.
<i>Pardosa purbeckensis</i>	98.5 $\pm$ 23.80	41.72 $\pm$ 7.70	5.13	*
Spider densities				
<i>Arctosa fulvolineata</i>	0.03 $\pm$ 0.03	0.43 $\pm$ 0.12	9.71	**
<i>Pardosa purbeckensis</i>	3.93 $\pm$ 1.24	1.37 $\pm$ 0.27	4.09	*

(Topping & Luff 1995). Traps were covered with a raised wooden roof to keep out rain. Catches in pitfall traps were related to trapping duration and pitfall perimeter, which calculates an 'activity trapability density' (number of individuals per day and per meter: Sunderland et al. 1995). Four pitfall traps were installed at each station and spaced 10 meters apart, considered as the minimum distance for avoiding interference between traps for spider catches (Topping & Sunderland 1992). Activity trapability density of spiders was followed during the entire period of activity of the two species from April–November 2002 except during high tides (Table 1).

**Spider densities:** To compare absolute densities of the two lycosids, 1m  $\times$  1m plastic quadrats (1 m height) were used. Quadrats were sampled by regular hand catches and pitfall traps (one placed in the middle of the quadrat) until there were no more individuals. Eight spatial replicates were sampled in each vegetation type (i.e. invasive and natural), and this technique was used four times in June and July 2003 (i.e. 32 replicates per vegetation: Table 1).

**Effects of flooding:** To determine the role of vegetation cover in modifying species ability to resist flooding, spiders were sampled before and after a spring tide (tidal range: 13.35 m) in April 2004 (Table 1). Three natural and three invaded stations were studied at three salt marsh levels ranging from the high to the low marsh (i.e. 50, 150 and 200 meters from the dike). Four pitfall traps per station were activated during three consecutive days before and after the high tide. Catches were completed by hand collecting during activation and collection of pitfall traps for a total of 1.5 hours per station before and after the high tide.

### Characterization of natural and invaded habitats.

**Abiotic characteristics:** To characterize plant communities, vegetation was described four times within a radius of 1 m around each pitfall trap (4 replicates per station) at the 'Ferme Foucault' site: litter depth (to the nearest mm) and vegetation height (to the nearest cm). Soil salinity (estimated by pore water electrical conductivity), soil water content and temperature were measured using a W.E.T. Sensor connected to a moisture meter HH2 (Delta-T Devices Ltd., Cambridge, UK) and made with a specific clay soil calibration. All abiotic variables were assessed in summer 2002 (Table 1). Soil temperatures were measured at 11h a.m. to compare this micro-climate parameter between habitats, but not to characterize it along time.

**Biotic characteristics:** Food resources were estimated by vertical sampling using a soil core (12 cm depth and 10 cm for diameter), except for the very mobile amphipod (see below). Six cores were collected in each habitat (natural or invaded) during October 2003 (Table 1). Cores were then sieved through a 250  $\mu$ m mesh screen. Because cannibalism and intraguild predation are a general rule in spiders, especially in structurally simple ecosystems (e.g., Schaefer 1974), spider densities were included in total arthropod densities when comparing the food resources between invaded and natural areas. The results do not include an important macrofauna component, the gastropod *Phytia bidentata* because this species is not likely to be consumed by the two lycosid species.

Because the amphipod *Orchestia gammar-ella* represents one of the more abundant arthropods in west European salt marshes (e.g., Meijer 1980), special attention was paid to



Table 3.—Comparison of mean activity abundances measured by pitfall traps (number of individuals/day/meter; in parentheses: total number of individuals) before and after the high tide in natural and invaded stations, and statistical comparisons using ANOVA (Code: n.s. = non significant, \* =  $P < 0.05$ , \*\* =  $P < 0.01$ ).

	Species abundances		<i>F</i> -ratio	Code
	Before the high tide	After the high tide		
Natural stations				
<i>Arctosa fulvolineata</i>	1.77 ± 0.49 (40)	0.44 ± 0.21 (18)	6.14	*
<i>Pardosa purbeckensis</i>	3.36 ± 1.14 (364)	2.12 ± 0.47 (274)	1.00	n.s.
Invaded stations				
<i>Arctosa fulvolineata</i>	0.97 ± 0.28 (31)	0.80 ± 0.27 (23)	0.21	n.s.
<i>Pardosa purbeckensis</i>	4.69 ± 1.06 (214)	2.03 ± 0.51 (163)	5.04	*

this species. Densities of *O. gammarella* were calculated in natural and invaded habitats using a depletion method. Within each plant community, four 1m<sup>2</sup> quadrats were randomly sampled in June 2003 by hand catches and pitfall traps until there were no more individuals.

To measure nocturnal and diurnal wanderer densities, spider densities were estimated by the quadrat-flotation technique. Homogeneous 0.25 m<sup>2</sup> areas were isolated by iron quadrats (0.5 meter width and 1 meter height) set into the ground to a depth of 0.20 m. All vegetation was removed, stored in sealed bags and analyzed in the laboratory. The spiders remaining within the quadrat were then hand collected on the bare soil until none were visible. A pitfall trap was placed in the middle of the quadrat and left in place until all remaining moving individuals were caught. A last hand collection was also carried out during the time of pitfall trapping. The spider density was calculated by summing individuals of the initial and final hand collections with the catches of both pitfall trap and vegetation samplings. Four replicates were performed at each station and repeated four times during June 2002 (Table 1).

**Identification and data analyses.**—All the spiders collected were preserved in 70% ethanol, transported to the laboratory for species identification and kept in the University collection (Rennes, France). In the tables, all means are presented with standard error (mean ± s.e.). Mean environmental and species variables were compared using ANOVA tests after verification of normal distribution according to Kolmogorov-Smirnov tests (MINITAB).

RESULTS

**Comparison of habitat preference.**—Catches by pitfall traps revealed that *Pardosa purbeckensis* activity abundances were significantly higher in natural than in invaded plots (Table 2). In accordance with trends found in activity, *P. purbeckensis* had a significantly higher density in natural plots. However, *Arctosa fulvolineata* had much higher densities in invaded than in natural plots, whereas its abundance did not differ significantly between the two vegetation types (Table 2).

**Comparison of flooding effects between natural and invaded vegetation.**—Based on their distribution change after the high tide, *Arctosa fulvolineata* and *Pardosa purbeckensis* presented similar reactions to flooding, with an unmodified distribution (in terms of presence/absence) in natural and invaded stations. Only *A. fulvolineata* almost disappeared from one natural station (level 2), where less than 5 individuals were caught after the high tide. In fact, this species presented comparable abundances before and after the high tide in invaded stations (Table 3), whereas its mean abundance significantly decreased in natural stations. *Pardosa purbeckensis* showed significantly decreased abundances after the high tide in invaded stations and constant abundances in natural stations (Table 3).

**Comparison of habitat characteristics.**—Invaded stations (*Elymus athericus*) differed significantly from natural stations (*Atriplex portulacoides*), i.e. they had deeper litter and taller plant cover (Table 4). No significant differences were found regarding soil salinity, soil water content and temperature. Regarding

potential prey, Acari and Amphipoda (*Orchestia gammarella*) densities were significantly lower in invaded areas, leading to a decrease in total pedofauna at these stations (Table 4). No significant difference was found for Collembola.

Species from the guild of *Pardosa purbeckensis* (diurnal wanderers) were found in significantly higher densities in invaded than in natural stations (the more dominant species were the non-coastal *Pardosa prativaga*, *P. proxima* and *P. pullata*), whereas no difference between vegetation types was found for species from the *Arctosa fulvolineata* guild (nocturnal wanderers, mainly including the non-coastal *Agroeca lusatica*, *Clubiona stagnatilis* and *Zelotes latreillei*).

## DISCUSSION

**Changes in habitat characteristics after *Elymus* invasion.**—Lycosids in general and the genus *Pardosa* in particular are known to prefer open habitats (e.g., Aart 1973), and Harvey et al. (2002) suggested that adults of *P. purbeckensis* are favored by low vegetation. Kessler & Slings (1980) demonstrated the tendency among juveniles of *P. purbeckensis* to aggregate and to select grass with high shoot densities, probably to avoid cannibalism. Because more diurnal wandering spiders are hunting in invaded plots, we suggest that young specimens of *P. purbeckensis* are exposed to a higher predation risk than in natural areas, contributing to the lower adult density in the invaded areas. Thus we propose that the habitat structure of *Elymus* (mainly tall vegetation and deep litter) was not suitable for this species and contributed to its lower occurrence in invaded habitats. In contrast, *Arctosa fulvolineata* might be favored by the structure of the invaded habitats: a deeper and more complex litter due to a lower rate of *Elymus* litter decomposition (Valéry et al. 2004). As a general rule, deep litter, by providing new microhabitats and microclimate conditions (Wise 1993), tends to favor nocturnal wanderers (case of *Arctosa fulvolineata*), ambush hunters (thomisids) and “litter-sensitive” sheet-weavers (Bell et al. 2001). Thus we suggest that *A. fulvolineata* prefers more heterogeneous litter of invaded areas, where it is often found during the day, at 3–4 cm depth (Pétillon pers. obs.).

Differences in the responses of dominant

salt marsh species to the invasion can be influenced by many other factors than abiotic components of habitats. In particular for simple ecosystems such as salt marshes, interspecific competition may reduce spider populations (Schaefer 1972 according to Wise 1993; Marshall & Rypstra 1999). We propose that invaded habitats, by hosting other species from the same guild as *P. purbeckensis* (especially *Pardosa prativaga*, *P. proxima* and *P. pullata*), increased inter-specific competition. Contrary to *P. purbeckensis*, *A. fulvolineata* seemed not to be subjected to higher levels of competition in invaded habitats, as nocturnal wanderer densities were the same in natural and invaded habitats. Little is known about salt marsh spider diets, except predation upon Collembola for *P. purbeckensis* (Schaefer 1974) and for the linyphiid *Erigone arctica* (White 1852) (Legel & Wingerden 1980). So, at the moment there is no evidence for food limitation, even if some potential prey decreased in invaded habitats (e.g., the amphipod *Orchestia gammarella*).

**Changes in flood resistance in invaded habitats.**—In this study, the two salt marsh species responded differently to flooding in invaded habitats. *Pardosa purbeckensis* abundances decreased only in invaded stations after the high tide. If this species uses underground refuges during flooding, as do several intertidal invertebrates (Foster & Treherne 1976; Kneib 1984), then it would be disfavored in invaded areas (deep but thin roots of *Elymus*) compared to natural areas (short and large roots of *Atriplex portulacoides*). Contrary to *P. purbeckensis*, *A. fulvolineata* seem to derive benefits from the invasive plant because its abundance remained the same after the high tide in the invaded stations and decreased in the natural stations. This litter-living species might be favored by *Elymus* *athericus* that seems to improve its habitat by increasing the food resources and the amount of air in the litter.

**Conflicting aspects of the grass invasion: how to manage it.**—Habitat suitability of natural and invaded areas clearly differed between the two wolf spiders. Activity trappability density of *P. purbeckensis* was strongly reduced in invaded areas indicating a decrease in the density and/or the mobility of individuals, whereas activity trappability density of *A. fulvolineata* was enhanced in invaded sta-



Table 4.—Habitat characteristics (mean ± s.e.) of natural and invaded stations, and statistical comparisons using ANOVA (Code: n.s. = non significant, \* =  $P < 0.05$ , \*\* =  $P < 0.01$ ).

	Units	Natural plots	Invaded plots	F-ratio	Code
Structural components					
Vegetation height	cm	29 ± 0.63	78 ± 1.64	331.43	**
Litter depth	cm	0	4 ± 0.23	754.60	**
Soil water content	%	60.13 ± 4.21	57.72 ± 1.12	0.31	n.s.
Soil salinity	mS/m	1009.7 ± 50.1	1013.8 ± 45.1	<0.01	n.s.
Soil diurnal temperature	°C	10.86 ± 0.62	11.00 ± 0.38	0.03	n.s.
Biotic components					
Amphipoda	Number/m <sup>2</sup>	979 ± 311	205 ± 51	6.02	*
Acari	Number/m <sup>2</sup>	55302 ± 8688	20202 ± 3085	14.49	**
Collembola	Number/m <sup>2</sup>	5008 ± 2391	5645 ± 2574	0.03	n.s.
Total pedofauna	Number/m <sup>2</sup>	60352 ± 7053	26293 ± 3707	18.27	**
Diurnal wanderers	Number/m <sup>2</sup>	6.50 ± 2.10	29.25 ± 6.97	9.77	*
Nocturnal wanderers	Number/m <sup>2</sup>	0.75 ± 0.48	5.25 ± 2.78	2.54	n.s.

tions. Here, quadrat results confirmed that changes in activity trappability densities also reflected changes in the species' population densities.

More than ten years after the grass invasion, the two dominant halophilic species are still present in invaded salt marshes (Fouillet 1986; present study). But our results indicate that in the near future microhabitat changes and (perhaps) competition for space and food between native and non-coastal (immigrated after the *Elymus* invasion) species could lead to a decline in the absolute density of the dominant native species such as *Pardosa purbeckensis*. This is a unique case of an invasion which involves, as it seems at the moment, both positive and negative aspects for dominant halophilic spiders, enhancing one species and reducing the other! As similar invasions are affecting more and more salt marshes in Western Europe (Bockelmann & Neuhaus 1999), we suggest that management plans should be undertaken for reducing the paradoxical consequences of *Elymus* invasion on typical and rare salt marsh biodiversity. The effects of mowing are surveyed at the moment in the Mont Saint-Michel bay. By re-opening the soil, mowing seems to maintain healthy populations of both halophilic species. This is in contrast to sheep-grazing that is likely to only favor *P. purbeckensis*, and even tends to disfavor both dominant halophilic wolf spiders when practiced in a too intensive way (Pétillon et al. submitted).

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## THE DIET OF THE CAVE SPIDER *META MENARDI* (LATREILLE 1804) (ARANEAE, TETRAGNATHIDAE)

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**ABSTRACT.** This study investigated the range and number of prey consumed by a population of *M. menardi* in an abandoned mine drainage adit at Mary Tavy, on the edge of Dartmoor (Devon, UK). The adit was visited each week from October 1997 to November 1998 and any spider found feeding was interrupted and its prey removed and preserved in alcohol. Over the 13 months a total of 69 prey were recovered representing 18 taxa. While a number of flying insects used the adit as a refuge in which to over winter they formed a small percentage of the total prey consumed. Most of the prey were members of the soil or litter fauna (myriapods and slugs) that were observed walking over the surface of the adit walls.

**Keywords:** *Meta menardi*, prey, myriapods, slugs, litter fauna

*Meta menardi* (Latreille 1804) is a well known member of the twilight zone community in subterranean systems. This zone is located just beyond the entrance and provides an environment buffered from the extremes of the outside world while still receiving light from the external environment. As such, this zone forms a series of small habitat islands on the fringes of subterranean systems. While this habitat is connected to the external environment, the dark entrance zone acts as a significant barrier to many invertebrates, thus the diversity of potential prey in the twilight zone is low by comparison with the outside. Predators that occupy this zone are isolated from the surrounding habitats and thus have access to a limited range of potential prey. Yet as populations of *M. Menardi* can be large (in excess of a 100 individuals, pers. obs.), it is clear that an abundance of prey must be available in order to sustain populations of this size.

A number of invertebrates have been previously recorded as prey of *M. menardi*. Yoshida & Shinkai (1993) recorded Diplopoda, Diptera, Formicidae and Vespidae from a population living between boulders in Japan, while both Eckert & Moritz (1992) and Chapman (1993) recorded myriapods, Coleoptera and isopods as prey from populations in Germany and the UK respectively. Previous studies by the author recorded 2 species of diplopods, 1 isopod, carabid beetles, spiders of

the genus *Meta*, plus slugs and oligochaetes (Smithers 1996). Studies of a cellar population in Germany revealed; 9 spp. Coleoptera, 2 spp. Isopoda, 3 spp. Araneae, 2 spp. Diptera, 1 spp. Gastropoda, 2 spp. 1 spp. Opiliones, Chilopoda, 1 spp. Nematophora, 1 spp. Hymenoptera and 1 spp. Pseudoscorpiones (Pöttsch 1966).

While previous work has shown that *M. menardi* consumes a wide range of prey there has not been a systematic study of the relative abundance of these prey in the diet of this species or an investigation of any seasonal variation. This study was designed to investigate the diet of *M. menardi*, and to determine any seasonal or life stage variations in the prey consumed.

### METHODS

The work was conducted in an abandoned mine drainage adit on the edge of Dartmoor, Devon, UK (SX 513787). A man-made tunnel was chosen due to its linear nature which meant that all members of the population were accessible for observations. The adit was situated in a steep bank, the top of which was covered with deciduous woodland. The site was visited each week from October 1997–November 1998 (no data was gathered between December 97–January 98). At each visit the population was examined for spiders with prey in their web or mouthparts. When spiders with prey were disturbed the spider

Table 1.—The abundance of prey groups recovered from different life stages of *Meta menardi*.

Prey taxon	Immature	Female	Male	Total	% of total
Unidentified prey items	1	2		3	4
Diptera, Nematocera	2	1		2	3
Diptera, Culicidae	1			1	1
Diptera, <i>Eristalis</i> sp.			1	1	1
Coleoptera, Carabidae	2	3		5	7
Trichoptera unidentified	5	4		9	13
Trichoptera, <i>Stenophylax permistus</i>		1		1	1
Trichoptera, pupae		1		1	1
Neuroptera, Sisyridae		1		1	1
Lepidoptera, <i>Scoliopteryx libatrix</i>		1		1	1
Araneae, imm <i>Meta menardi</i>	1	1	1	2	3
Araneae, <i>Meta merianae</i>		2	1	3	4
Myriopoda, unidentified Diplopoda			1	1	1
Myriopoda, Julidae	5	5		10	14
Myriopoda, <i>Cylindroiulus punctatus</i>	1	2		3	4
Myriopoda, <i>Nanagona polydesmoides</i>	4	3		7	10
Myriopoda, Chilopoda Geophilomorpha	3			3	4
Gastropoda (Slugs)	1	12		13	19
Total number of prey recorded	26	39	4	69	

would retreat to the top of the web leaving the prey hanging by a silken thread. Any prey discovered were removed and taken back to the laboratory where they were preserved in 70% alcohol, then identified to the lowest taxonomic unit possible. The prey recovered were always wrapped in silk and in an advanced state of digestion. The exoskeleton of the arthropods were broken open and fragmented while the molluscs were usually digested from one end, occasionally leaving a head or rear intact. All of the spiders sampled were assigned to one of three life stage groups, females, males or immatures. Voucher specimens of *M. menardi* collected at the study site have been lodged in the invertebrate collection at the University of Plymouth.

## RESULTS

A total of 69 prey were recovered representing 17 taxa, only 3 of which proved to be unidentifiable (Table 1). The myriapods were the most abundant prey recovered with 24 individuals, followed by slugs with 13 individuals, Trichoptera with 11, Araneae with 6 and Carabidae with 5. Other prey were recorded in small numbers (Table 1). It is clear that three taxa dominate the prey recovered over the sampling period. These are the myriapods, the gastropod slugs and the Trichoptera. Few prey were recovered from males while fe-

males and immature spiders were recorded consuming approximately equal numbers of most prey groups except slugs, which were primarily collected from females (only one slug was not taken from a female) (Table 1).

## DISCUSSION

The myriapod prey comprised three main taxa, julid millipedes (some of which could be identified as *Cylindroiulus punctatus*), *Nanagona polydesmoides* and the geophilomorph centipedes. The julids were more abundant in May (4 individuals) and in the autumn (October & November 2 individuals each) but were occasional prey at other times of the year (February & August 1 individual each). The slight increase in numbers captured in the spring and autumn could be explained by a seasonal vertical migrations in the litter/soil undertaken by julids as reported by Geoffroy (1981). While the autumn migration is downward, both the spring and autumn migrations would involve an increase in the activity of individuals. Given the proximity of the adit entrance to the soil litter interface, some individuals becoming active in the spring could reach the surface and follow the rock surface down into the adit entrance. The geophilomorph centipedes also displayed a small autumn peak which could also be explained by seasonal migrations down the soil profile.



*Nanagona* is also an occasional prey over the spring and summer, which is not surprising as this is a well known troglophile that is commonly encountered in subterranean chambers (Blower 1985; Chapman 1993).

The Trichoptera also displayed seasonal patterns of abundance, being abundant in April / May and again in August where they displayed a distinct peak. This was probably the result of an emergence of adults from either the river outside the adit or the stream within it (a single pupal Trichoptera was recorded, indicating that individuals were emerging within the adit).

The slugs were recovered in small numbers over the late spring through to the autumn in which they displayed a distinct peak. This peak may be a result of their seasonal migration down the soil profile to escape the harsher winter conditions. This would bring them into the mine adit via the micro caverns in the bed rock. Once at a safe depth they are then quiescent for the winter months, thus explaining their absence from the diet of *M. menardi* between December and April. At 19% of the prey captured (Table 1) gastropods are an important element in the diet of *M. menardi*. This is unusual for a spider as a recent review of malocophagy in spiders has shown *M. menardi* to be the only araneomorph spider to include gastropods as a regular part of its diet (Nyffeler & Symondson 2001).

While slugs have been observed crawling into water laden webs of *Argiope bruennichi* (Scopoli 1772) (Quicke 1987), the exact method of prey capture used by *M. menardi* is as yet unknown. The bias in the number of slugs recovered from females (Table 1) hints that this particular prey may require the larger body size exhibited by most females to successfully capture this prey. A similar bias has also been observed in some carabid beetles (Nyffeler & Symondson 2001). Further work is required to determine the exact nature of the prey capture method for this species.

The remaining prey were captured in low numbers through out the year. A number of flying insects such as the hover fly *Eristalis tanax*, the Golden caddis fly *Stenophylax permistus*, the herald moth *Scoliopteryx libatrix*, and mosquitoes of the genus *Culex* commonly use underground chambers as over-wintering sites (Chapman 1993). These can aggregate in

large numbers on the walls of underground chambers but, despite their presence in the adit these species were not common elements of *M. menardi*'s prey spectrum. This may be a reflection of their behavior, as they fly into the chamber and quickly settle on the walls where they become immobile until the following spring (pers. obs.). Unless they land in a web they are unlikely to attract a spider's attention.

Carabidae were recorded in the spring with a single record from the autumn. These are active predators that had probably strayed into the adit via the entrance from the woodland floor above. The spiders *Metellina meriane* (Scopoli 1763) and *M. menardi* were occasional prey over the spring and autumn, hinting that for any individual moving around within the chamber can be hazardous.

Predators that occupy the twilight zone have access to a range of potential prey which can be divided into three groups: organisms that move into the subterranean system from the external environment to seek shelter or over winter; those that move down the litter/soil profile and into the chambers via the micro and meso cavern network that connects the macro chambers with the overlying soil system; and members of the deep cave fauna that may stray into this zone. It appears that *M. menardi* has specialized in capturing members of the soil/litter fauna that stray in to underground chambers, but will respond opportunistically to any additional prey that walk over the inner surface of the underground chamber.

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## THE SPIDER FAUNA OF THE IRRIGATED RICE ECOSYSTEM IN CENTRAL KERALA, INDIA ACROSS DIFFERENT ELEVATIONAL RANGES

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**ABSTRACT.** A survey of spiders associated with the irrigated rice ecosystem in central Kerala, India was conducted across different elevational ranges. Spiders were collected from rice fields of high ranges, midland and low land areas in two cropping seasons viz., June–September 2002 (Kanni Krishy) and October 2002–February 2003 (Makara Krishy) with a total of 144 hours of sampling time distributed across the two seasons. The sampling areas constituted Adimali and Marayoor of Idukki district (high range), Vannappuram of Idukki district and Kothamangalam of Ernakulam district (midland) and Parakkadavu and Piravom of Ernakulam district (lowland). Visual searching methods were used to sample the spider fauna from quadrats. A total of 1130 individuals belonging to 92 species, 47 genera and 16 families were recorded during the study period. Araneidae and Tetragnathidae were the dominant families and *Tetragnatha mandibulata* Walckenaer 1842 (Family Tetragnathidae) the most abundant species. Various diversity indices, as well as richness and Chao I estimator were used to analyze the possible effect of elevation on species occurrence; the results showed that species richness and diversity were the highest in Parakkadavu, which is a lowland area. In a cluster analysis the localities belonging to the same elevation were found to form separate groups. The species fell into seven feeding guilds. Orb weavers were dominant at all study sites.

**Keywords:** Araneae, central Kerala, diversity, elevational gradient.

Spiders are ubiquitous in terrestrial ecosystems and abundant in both natural and agricultural habitats (Turnbull 1973; Nyffeler & Benz 1987). They play an important role in regulating insect pests in agriculture ecosystems (Nyffeler & Benz 1987; Nyffeler et al. 1994; Sunderland 1999). Studies of Hamamura (1969), Sasaba et al. (1973), Gavarra & Raros (1973), Samal & Misra (1975), Kobayashi (1977), Chiu (1979), Holt et al. (1987) and Tanaka (1989) clearly described the role of spiders as predators in reducing insect pests

in rice fields. In India, studies on the population and abundance of the spider assemblages in agricultural crops are few. Some basic studies were carried out by Pathak & Saha (1999) and Bhattacharya (2000). Banerji et al. (1993) and Anbalagan & Narayanaswamy (1999) also analyzed the population fluctuation of spiders in paddy fields. However, these studies were mostly limited to the identification of spiders and investigation of the dominant spider species. In this paper, we document the araneofauna associated with the irrigated rice

(*Oryza sativa* L.) ecosystem in central Kerala, India, based on studies conducted during two crop seasons. We also attempted to compare the diversity and richness of spiders across different elevational ranges and to analyze the possible effect of elevation on species occurrence.

## METHODS

**Study Area.**—The areas selected for the study belong to Ernakulam and Idukki districts in Central Kerala, India. Elevation in these two districts ranges from 0–2695 m above MSL. The sampling sites included Adimali (latitude 10° 5' N; longitude 77° 44' E; elevation 1100 m above MSL) and Marayoor (10° 5' N; 77° 4' E; 2100 m above MSL) of Idukki district in the high range; Kothamangalam of Ernakulam district (9° 58' N; 76° 34' E; 230 m above MSL) and Vannappuram of Idukki district (9° 54' N; 76° 43' E; 270 m above MSL) in midland; and Parakkadavu (11° 15' N; 75° 49' E; 11 m above MSL) and Piravom (9° 58' N; 76° 34' E; 30 m above MSL) of Ernakulam district in the lowland. Average annual rainfall in Ernakulam district is 343.2 cm with 139 rainy days. Temperature ranges from 20–35 °C. The western parts of Idukki district comprising the midland area experiences moderate climate, temperature varying between 21–27 °C with minimum seasonal variation. The eastern parts of the district located in the highland have a comparatively cold climate with temperature varying between minus 1–15 °C in November/January and 5–15 °C during March/April. The sampling units were selected at random in all the localities.

The rice ecosystem in central Kerala consists of two physically and morphologically distinct habitats; the rectangular shaped flooded fields vegetated mainly by the rice plants, and the surrounding bunds which harbor weeds. This mosaic system is connected with irrigation canals and ditches, while sump ponds, marshes and tanks serve as contiguous aquatic habitats. The rice fields are frequently disturbed by farming practices, i.e. tillage, irrigation, fertilization, crop establishment, weeding and pesticide application, and by natural phenomena such as rainfall and flooding. These disturbances result in extreme instability on a short time-scale during the crop cycle, but relative stability on a long time-scale (Wa-

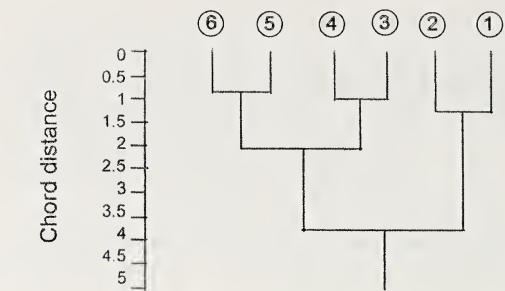


Figure 1.—Dendrogram for the cluster analysis of six sampling sites. 1 = Parakkadavu, 2 = Piravom, 3 = Vannappuram, 4 = Kothamangalam, 5 = Adimali, 6 = Marayoor.

tanabe & Roger 1985). Although rice is infested by a multitude of insect pests, the most destructive of them in central Kerala are the rice bug, *Leptocoris acuta* (Thunberg); green leafhopper *Nephotettix virescens* (Distant) and brown planthopper, *Nilaparvata lugens* (Stal).

**Study Time.**—The study was carried out in two cropping seasons, viz. June–September 2002 (Kanni Krishy) and October 2002–February 2003 (Makara Krishy). A total of 144 hours were spent for sampling distributed across both cropping seasons.

**Sampling.**—Visual search was used for sampling in each selected study site. We spent one hour in each sampling unit on a fortnightly basis during each cropping season. Sampling was done from the same field during both seasons. A total of 24 hours were spent in each site across both cropping seasons, totaling 144 hours of sampling time. Spiders were collected from four quadrats (1 m x 1 m) placed at the four corners of a 10 m x 10 m area. Collections were done during early morning hours since it was observed that spider activity was the maximum at that time of day in the rice fields and the morning-dew-covered webs were easy to observe. The area around each plant was searched for possible webs and the plants were thoroughly examined for spiders from the bottom to the top. The spiders collected from each site every fortnight were preserved together in 70% ethyl alcohol with proper labeling of locality, date of collection and other notes of importance. The preserved specimens were counted under a stereo-zoom microscope (Leica-MS5). Spiders of all life stages were collected during sampling. The spiders were identified to the



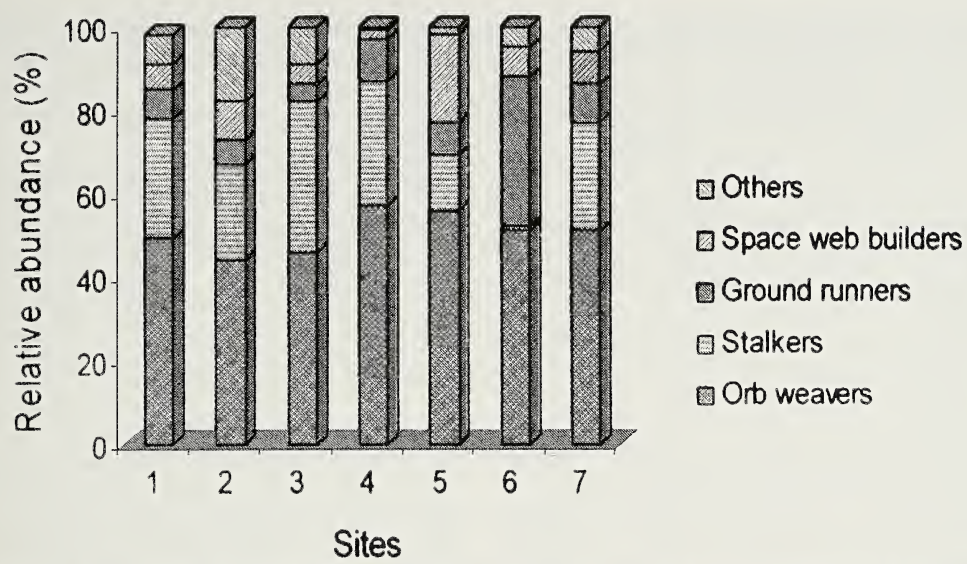


Figure 2.—Percentage of spider species by feeding guilds collected from irrigated rice ecosystem in central Kerala, India. 1 = Parakkadavu, 2 = Piravom, 3 = Vannappuram, 4 = Kothamangalam, 5 = Adimali, 6 = Marayoor, 7 = Total.

species level with the help of available literature (Tikader 1987; Barrion & Litsinger 1995) except the immature ones, which could be identified only to the generic level. Voucher specimens were deposited in a reference collection housed with the Arachnology Division, Dept. of Zoology, Sacred Heart College, Cochin, Kerala, India.

**Data Analysis.**—The diversity of spiders across different elevations were analyzed by widely used indices viz., the Shannon-Wiener index, which is sensitive to changes in the abundance of rare species in a community, and the Simpson index, which is sensitive to changes in the most abundant species in a community (Solow, 1993). Shannon-Wiener index is defined as:

$$H' = -\sum p_i \log p_i$$

where  $p_i = n_i/N$  is the observed relative abundance of a particular species;  $n_i$  = the number of individuals of species  $i$ , and  $N = \sum n_i$ . The Simpson index is defined as:

$$D = \frac{\sum n_i(n_i - 1)}{N(N - 1)}$$

The results are given as 1-D.

The Margalef index, a species richness index, was computed based on the relationship between species richness (S) and total number

of individuals observed (N) which increases with increasing sample size. The Margalef index:

$$R1 = S - 1/\ln N.$$

The evenness index is a measure of how evenly species are distributed in a sample. When all species in a sample are equally abundant an evenness index will be at its maximum, decreasing towards zero as the relative abundance of the species diverge away from evenness. The modified Hill's ratio (E5) is the best evenness index, the least ambiguous, the most easily interpreted and is independent of the number of species in the sample (Ludwig & Reynolds 1988):

$$E5 = (1/D) - 1/e^{H'} - 1$$

where D = Simpson's index and  $H'$  = Shannon-Wiener index.

The Shannon-Wiener, Simpson, Margalef and Evenness (E5) indices were computed using the statistical software, SPDIVERS.BAS of Ludwig & Reynolds (1988).

The estimated species richness was calculated to determine whether or not the environment had been sufficiently sampled. The Chao 1 quantitative estimator (Chao 1984; Colwell & Coddington 1994) is calculated as:

$$S_{Chao1} = S_{obs} + (a^2/2b)$$

Table 1.—Total number of families, genera, and species composition of spiders sampled from different localities of central Kerala. 1 = Parakkadavu, 2 = Piravom, 3 = Vannappuram, 4 = Kothamangalam, 5 = Adimali, 6 = Marayoor.

Family	Genera	Species	Individuals	Localities					
				Lowland		Midland		Highland	
				1	2	3	4	5	6
Araneidae	11	25	132	9	5	13	12	13	9
Clubionidae	1	2	4	1	1			1	1
Eresidae	1	1	1						1
Filistatidae	1	1	1				1		
Gnaphosidae	1	1	2	1	1				
Hersiliidae	1	1	2	1			1		
Linyphiidae	1	1	59	1	1	1		1	1
Lycosidae	3	7	107	6	4	6	6	6	5
Miturgidae	1	1	2	1					
Oxyopidae	2	9	171	6	2	8	6	3	
Salticidae	10	14	115	10	3	5	10	5	
Sparassidae	1	1	1	1					
Tetragnathidae	4	16	437	12	4	10	13	13	7
Theridiidae	7	8	85	7	5	3	3	2	3
Thomisidae	1	2	4	2	1	1			
Uloboridae	1	2	7						1
Total	47	92	1130	58	27	47	54	44	28

where  $S_{obs}$  is the number of species observed; a is the number of singletons and b is the number of doubletons. The EstimateS program (Colwell 2000) was used to calculate the Chao 1.

The degree of association or similarity of the sampling sites was investigated using cluster analysis. The term “cluster analysis” encompasses a number of different classification algorithms (Faith 1991). It is a useful data reduction technique that can be helpful in identifying patterns and groupings of objects. The program CLUSTER.BAS (Ludwig & Reynolds 1988) was used for the cluster analysis of the data from different localities using the flexible strategy (Lance & Williams 1967) and chord distance, a measure of dissimilarity.

RESULTS

**Distribution.**—Spiders representing 16 families, 47 genera and 92 species were recorded during the study (Appendix 1). Table 1 is a summary of family composition. The sampling yielded a total of 1130 individuals. Some families were widely distributed throughout the study area while others were restricted to one or a few localities. The widely distributed families were Araneidae, Lycosidae, Tetragnathidae and Salticidae. Family

Araneidae was represented by 25 species belonging to 11 genera. However, the numerically dominant family was Tetragnathidae with a collection of 437 individuals belonging to 16 species and 4 genera. The numerically most abundant species was *Tetragnatha mandibulata* Walckenaer 1842 (Family Tetragnathidae) with a total of 109 individuals (Appendix 1). *T. javana* (Thorell 1890), *T. cochinesis* Gravely 1921, *Tetragnatha* sp., *Pardosa pseudoannulata* (Bösenberg & Strand 1906), *Pardosa* sp., *Lycosa tista* Tikader 1970, *Argiope* sp., and *Chrysso argyrodiformis* (Yaginuma 1952) were present at all study sites.

**Diversity.**—Diversity measurements did not vary considerably between sites across elevational gradients (Table 2) although the Parakkadavu site in the lowland recorded the highest Shannon-Wiener (3.49), Simpson (0.96), Margalef (6.83) and richness (58) values. The Evenness index E5 was the highest at Marayoor (0.90). The Chao 1 species richness estimator generated species richness values which were higher than the actual richness values. The highest value was observed at Parakkadavu (91.1), whereas the actual richness value at this site was 58.



Table 2.—Species diversity measures of spiders in rice ecosystem sampled from different localities in central Kerala. 1 = Parakkadavu, 2 = Piravom, 3 = Vannappuram, 4 = Kothamangalam, 5 = Adimali, 6 = Marayoor.

Diversity measures	Lowland		Midland		Highland	
	1	2	3	4	5	6
Shannon-Wiener index ( $H'$ )	3.49	2.82	3.22	3.46	3.17	3.01
Simpson index (1-D)	0.96	0.92	0.93	0.95	0.93	0.94
Margalef index ( $R_1$ )	6.83	3.92	6.00	6.71	5.73	4.21
Evenness index ( $E_5$ )	0.86	0.85	0.84	0.87	0.84	0.90
Richness ( $S$ )	58	27	47	54	44	28
Chao 1	91.1	33.9	61.3	68.3	68.4	41.2

**Cluster Analysis.**—The pattern of clustering for the six localities is summarized in the dendrogram in Fig. 1. The species level analysis revealed two main clusters. The first cluster included four sites; Vannappuram and Kothamangalam (mid land) and Adimali and Marayoor (high land). At a chord distance of approximately 2.5, two groups emerged from this cluster. The first group was formed of the two high land sites while the second group included the two mid land sites. The second cluster was occupied by the remaining two low land sites, Parakkadavu and Piravom.

**Guild Structure Analysis.**—The spiders sampled belong to seven different foraging guilds (Uetz et al. 1999). These guilds are orb weavers, stalkers, ground runners, space web builders, sheet web builders, foliage runners, and ambushers (Fig. 2). Even though substrata for anchoring the webs are limited in rice fields compared to other terrestrial habitats, the orb weavers dominated in all the locations constituting 51% of the total collection. Stalkers were also seen in abundance (26%). Ground runners and space web builders were represented by 9% and 8%, respectively. Space web builders, foliage runners, and ambushers were less common in the study area.

DISCUSSION

The sixteen spider families recorded from the rice fields of Central Kerala represent 37% of the families reported from the country (Tikader 1987). A total of 92 spider species were reported from the rice ecosystem of central Kerala using two identification keys. Use of only two keys provided by Tikader (1987) and Barrion & Litsinger (1995) is justified as they are sufficient to identify spiders found in peninsular India. In a similar study, Bambarade-

niya & Edirisinghe (2001) have documented 60 species of spiders from an irrigated rice field ecosystem in Sri Lanka. Other works in Southeast Asia include that of Heong et al. (1991) recording 46 species of predators including bugs and spiders in Philippine rice fields and Barrion & Litsinger (1995) recording about 342 species of spiders from rice fields in the Philippines and other Southeast Asian countries. The observation that Araneidae and Tetragnathidae are the largest families is in conformity with the findings of Bambaradeniya & Edirisinghe (2001) in the rice fields of Sri Lanka. The dominance of tetragnathid spiders in the rice ecosystem of central Kerala might be expected as this wet habitat provides the congenial habitat for this family.

An analysis of various diversity indices across different elevations yielded only minimal differences in most of the indices used. This suggests that the effect of elevation on the diversity of spiders is not very drastic in the rice ecosystems of central Kerala. Nonetheless, Parakkadavu, which is a lowland area, exhibited more overall species richness and diversity. There are many environmental factors that affect species diversity. Some of these factors include seasonality, spatial heterogeneity, competition, predation, habitat type, environmental stability and productivity (Rosenzweig 1995). In terrestrial environments, a decrease in species richness with elevation and latitude is a common phenomenon. High elevation communities almost invariably occupy smaller areas than lowlands and they will usually be more isolated from similar communities than lowland sites. The effects of area and isolation are certain to contribute to the decrease in species richness with

elevation (Townsend et al. 2002). This explains the high overall species richness and diversity of Parakkadavu in comparison with other sites selected for the study. In addition, at Parakkadavu, rice cultivation is practiced in a cyclical way between polycultures of bananas and vegetables. This practice will provide enough shelter for spiders in different seasons. However, reasons for the low diversity indices recorded in the other lowland site, Piravom, need to be determined. One reason could be the practice of monoculture prevailing in this locality.

From the dendrogram, it is evident that the localities belonging to the same elevation formed one group in the cluster analysis. The midland and high range sites were found to be similar in the occurrence of species. Clustering revealed that the two low land sites behaved as a separate entity from the rest of the sites in species composition. This trend was predictable also because the distance between the mid and high land sites were less than that between the mid and low land sites.

The maximum number of species estimated by Chao 1 quantitative estimator showed wide deviations from the observed number of species. Chao 1 is an abundance-based estimator, so the number of times a species is present in a sample set has a significant effect on the number of species estimated to be present. This explains why Chao 1 gave a larger estimate of the overall species richness in the selected sites. Also, the presence of singletons and doubletons caused the Chao 1 to behave erratically. High relative percentages of singletons and doubletons during a sampling period indicate low abundance with Chao 1 (Fassbender 2002). The difference in estimated and observed numbers of species using Chao 1 reveals that the sampling efforts used were inadequate to reveal the true species diversity at the sites and indicates the necessity to conduct more intensive studies with modification of sampling techniques, viz. including extended sampling time, sampling during different time periods of the day, etc.

The most common explanation for the observed pattern of spider guild structure is the nature of the host crop, including its structural diversity, microenvironment, or the level of disturbance. Ample observations and more recent experimental evidence suggest that habitat structure maintains a diverse spider as-

semblage (Uetz 1991) and may be critical to successful insect pest suppression. The structural complexity may determine the guild composition of a crop's spider fauna and indirectly influence the level of herbivore damage.

The rice ecosystem of central Kerala has a diverse spider community and further research is indicated to evolve a better understanding of their ecology. These studies should include exploring other factors which are important in influencing spider diversity and richness in this agroecosystem, viz. effects of insecticides, availability of prey species, intra- and interspecific competition, surrounding habitats and climatic factors.

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Appendix 1.—Abundance data (total catches of two seasons) for spiders of rice ecosystem of central Kerala. 1 = Parakkadavu, 2 = Piravom, 3 = Vannappuram, 4 = Kothamangalam, 5 = Adimali, 6 = Marayoor.

Species name	Localities						Total
	Lowland		Midland		Highland		
	1	2	3	4	5	6	
Family Araneidae							
<i>Araneus</i> sp.	8	2	3	8			21
<i>Araneus bilunifer</i> Pocock 1900	1						1
<i>Araneus ellipticus</i> (Tikader & Bal 1981)			1		3	1	5
<i>Argiope</i> sp.	2	2	1	3	1	2	11
<i>Argiope aemula</i> (Walckenaer 1842)		3	2	1	1	1	8
<i>Argiope anasuja</i> Thorell 1887			3				3
<i>Argiope catenulata</i> (Doleschall 1859)	3		1	1	3	2	10
<i>Argiope pulchella</i> Thorell 1881			1	2	1		4
<i>Chorizopes</i> sp.				1			1
<i>Cyclosa</i> sp.		1				3	4
<i>Cyclosa bifida</i> (Doleschall 1859)						1	1
<i>Cyclosa fissicauda</i> Simon 1889			1		1		2
<i>Cyrtarachne</i> sp.	1						1
<i>Cyrtophora</i> sp.	3	1		5	2		11
<i>Cyrtophora citricola</i> (Forskål 1775)					1		1
<i>Eriovixia</i> sp.				4			4
<i>Eriovixia laglaizei</i> (Simon 1877)				3			3
<i>Eriovixia excelsa</i> (Simon 1889)				2	1	2	5
<i>Gasteracantha geminata</i> (Fabricius 1798)			2		1	3	6
<i>Gibbaranea bituberculata</i> (Walckenaer 1802)	2						2
<i>Neoscona</i> sp.	6		3	7	4		20
<i>Neoscona bengalensis</i> Tikader & Bal 1981					1		1
<i>Neoscona molemensis</i> Tikader & Bal 1981			1	1	1	1	4
<i>Neoscona vigilans</i> (Blackwall 1865)			1				1
<i>Zygiella</i> sp.	1		1				2
Family Clubionidae							
<i>Clubiona</i> sp.	1	1					2
<i>Clubiona drassodes</i> O. P. Cambridge 1874					1	1	2
Family Eresidae							
<i>Stegodyphus sarasinorum</i> Karsch 1891						1	1
Family Filistatidae							
<i>Pritha</i> sp.				1			1
Family Gnaphosidae							
<i>Gnaphosa</i> sp.	1	1					2
Family Hersiliidae							
<i>Hersilia savignyi</i> Lucas 1836	1			1			2
Family Linyphiidae							
<i>Linyphia</i> sp.	22	16	16		2	3	59
Family Lycosidae							
<i>Hippasa</i> sp.		1	2	2	2	3	10
<i>Lycosa</i> sp.	6	2	2	8	1	7	26
<i>Lycosa tista</i> Tikader 1970	1		1	1	1		4
<i>Pardosa</i> sp.	2	2	2	2	1	2	11
<i>Pardosa pseudoannulata</i> (Bösenberg & Strand 1906)	1	1	1	3	1	8	15
<i>Pardosa minuta</i> Tikader & Malhotra 1976	1						1
<i>Pardosa sumatrana</i> (Thorell 1890)	11		1	8	9	11	40
Family Miturgidae							
<i>Cheiracanthium melanostomum</i> (Thorell 1895)	2						2
Family Oxyopidae							
<i>Oxyopes</i> sp.	22	6	36	12	3		79
<i>Oxyopes ashae</i> Gajbe 1999	11		8	8	4		31



Appendix 1.—Continued.

Species name	Localities						Total
	Lowland		Midland		Highland		
	1	2	3	4	5	6	
<i>Oxyopes bharatae</i> Gajbe 1999			1	1			2
<i>Oxyopes sakuntalae</i> Tikader 1970			3				3
<i>Oxyopes shweta</i> Tikader 1970	2		1	4			7
<i>Oxyopes sitae</i> Tikader 1970	1		1				2
<i>Oxyopes sunandae</i> Tikader 1970	11		13	9			33
<i>Peucetia</i> sp.				2			2
<i>Peucetia viridana</i> (Stoliczka 1869)	2	4	5		1		12
Family Salticidae							
<i>Bavia</i> sp.	1			1			2
<i>Bianor</i> sp.	6		1	1			8
<i>Hasarius adansonii</i> (Audouin 1826)	4						4
<i>Hyllus</i> sp.	6		1	3	2		12
<i>Myrmarachne orientales</i> Tikader 1973	1			1			2
<i>Phintella</i> sp.			2				2
<i>Phintella vittata</i> (C. L. Koch 1846)		2		2	3		7
<i>Plexippus</i> sp.	2	1	2	4	3		12
<i>Plexippus paykulli</i> (Audouin 1826)	1			4			5
<i>Plexippus petersi</i> (Karsch 1878)	18	10	2	15	6		51
<i>Telamonia</i> sp.					1		1
<i>Telamonia dimidiata</i> (Simon 1899)	1			2			3
<i>Thiania</i> sp.				1			1
<i>Thyene</i> sp.	5						5
Family Sparassidae							
<i>Heteropoda venatoria</i> (Linnaeus 1767)	1						1
Family Tetragnathidae							
<i>Dyschiriognatha dentata</i> Zhu & Wen 1978	6			1	2	1	10
<i>Leucauge</i> sp.	7		3	2	3		15
<i>Leucauge bituberculata</i> Baert 1987	1		1	1	1		4
<i>Leucauge celebesiana</i> (Walckenaer 1842)		2		1	1		4
<i>Leucauge decorata</i> (Blackwall 1864)					2	6	8
<i>Leucauge pondae</i> Tikader 1970	13		2	11	4		30
<i>Tetragnatha andamanensis</i> Tikader 1977	18		6	8	3	1	36
<i>Tetragnatha ceylonica</i> O. P. Cambridge 1869	4		12	1	4		21
<i>Tetragnatha cochinchinensis</i> Gravely 1921	12	9	17	4	6	1	49
<i>Tetragnatha fletcheri</i> Gravely 1921						4	4
<i>Tetragnatha javana</i> (Thorell 1890)	19	11	8	12	8	7	65
<i>Tetragnatha mandibulata</i> Walckenaer 1842	32	12	10	36	19		109
<i>Tetragnatha maxillosa</i> Thorell 1895	1		2	1	1		5
<i>Tetragnatha</i> sp.	16		9	14	26	6	71
<i>Tetragnatha vermiformis</i> Emerton 1884	4						4
<i>Tylorida culta</i> (O. P. Cambridge 1869)				2			2
Family Theridiidae							
<i>Achaearanea</i> sp.		2	2	2	22		28
<i>Achaearanea durgae</i> Tikader 1970	2						2
<i>Argyrodes</i> sp.	1			1		1	3
<i>Chrysso argyrodiformis</i> (Yaginuma 1952)	9	1	7		16	4	37
<i>Dipoena</i> sp.	1	1					2
<i>Phycosoma martinae</i> (Roberts 1983)	1	1					2
<i>Theridion</i> sp.	4	3		1		1	9
<i>Theridula</i> sp.	1		1				2
Family Thomisidae							
<i>Thomisus</i> sp.	1	1	1				3
<i>Thomisus andamanensis</i> Tikader 1980	1						1
Family Uloboridae							
<i>Uloborus</i> sp.				2		1	3
<i>Uloborus danolius</i> Tikader 1969				4			4
Total	325	99	203	238	180	85	1130

## ECOLOGICAL PROFILES OF HARVESTMEN (ARACHNIDA, OPILIONES) FROM VITOSHA MOUNTAIN (BULGARIA): A MIXED MODELLING APPROACH USING GAMS

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**ABSTRACT.** The present study is based on a large-scale sampling program carried out in the area of Vitosha Mountain (Bulgaria). The ecological profiles of the Opiliones inhabiting the investigated area are modelled by a mixed approach, using Generalized Additive Models (GAMs) over a Multiple Correspondence Analysis (MCA, performed on the sites by environmental variables matrix) ordination plot. According to the literature data describing the harvestmen species from Vitosha Mountain, the most important factor determining the ecological classification of the Opiliones is the habitat type. The modelled ecological profiles revealed that the elevation contributes the most to the ecological characterization of the Vitosha harvestmen species, followed by the habitat type and moisture regime of the sampling localities. Few harvestmen species demonstrate preferences to the middle- and high-mountain zones, while the majority of harvestmen species are confined exclusively to the low-mountain zone. The different species showed different responses (most of them were linear, not unimodal) towards the environmental variables.

**Keywords:** Ecological type, ecological classification, Opiliones, Bulgaria, Generalized Additive Models, Multiple Correspondence Analysis

Traditionally, studies on Opiliones in Bulgaria have been predominantly faunistic and taxonomic (Staręga 1976; Martens 1978; Beron & Mitov 1996; Mitov 1987, 1994, 1995a, 1997a, 2001, 2002, 2003, 2004; Mitov & Stoyanov 2004), while data about the biology and ecology of the group are comparatively scarce and scattered through the faunistic literature (Staręga 1976; Martens 1978; Mitov 1986, 1995b,c, 1996, 1997b, 2000, in press; Mitov & Stoyanov 2004). Even on a European scale the ecological research on this animal group remains insufficient. However, the works of Todd (1949), Pabst (1953), Pfeifer (1956), Williams (1962), Kolosváry (1966b), Tischler (1967), Weiss (1975, 1978, 1984, 1996), Obrtel (1976), Curtis (1978), Weiss & Sárbu (1977), Hiebsch (1978), Bliss & Tietze (1984), Klimeš & Špičáková (1984), Klimeš (1987, 1990, 2002), Sechterová (1989), Platen (1991, 1996, 2000), Simon (1995), Novak et al. (2004), Komposch & Gruber (1999), Lymberakis et al. (in press) are specially dedicated

to various aspects of the harvestmen ecology. Additional ecological notes may be found in the mostly faunistic studies of Cîrdei & Bulimar (1960), Hiebsch (1972), Meijer (1972), Thaler (1979), Müller (1984), Komposch (1995, 1997a,b,c, 1999, 2000, 2001, 2004), Platen et al. (1991), Platen & Broen (2002), Metzen & Cölln (1998), Komposch & Gruber (2004), in annotated species lists.

Many of these publications contain ecological classifications of harvestmen species, based on their affinities towards certain environmental conditions. These classifications are often based on the subjective evaluation of the author. For example, *Lophopilio palpinalis* (Herbst 1799) has been described as “stenotopic?” (Komposch 1997a) on one hand, and as “moderately eurytopic” and “vertical-ubiquistic” (Kolosváry 1965; Komposch 1999) on the other. Further, investigators go into even more detail by classifying this species also as “hemiombrophilous/ombrophilous” (Pfeifer 1956; Weiss 1975; Bliss & Tietze



1984; Mitov & Stoyanov 2004), “psychrophilous” (Mitov & Stoyanov 2004), “hemihygrophilous/hygrophilous forest form” (Weiss 1975; Martens 1978; Geyer 1983; Bliss & Tietze 1984; Müller 1984; Platen et al. 1991, 1996, 2000; Komposch 1997a,b, 1999; Metzzen & Cölln 1998; Platen & Broen 2002). These categorizations may have a significant empirical background, but often the ecological type of a species is confusing without detailed reference to the analytical procedures that led to them. So the above mentioned discrepancies might be a manifestation of Kühnelt’s principle of regional stenoecy (e. g. Kühnelt 1965) or due to subjective error. Recently, with the development of more elaborate modelling techniques that permit a direct relation between the species and their environment, attempts have been made to directly explore the responses of harvestmen species to various environmental variables by employing multivariate techniques (Klimeš 1997; Muster 2001). Subjecting a significant amount of data from the Czech Republic to multivariate analytical procedures (such as TWINSpan and CCA), Klimeš (1997) concluded that the main factors explaining the variation of the data were elevation, temperature and human impact. Muster (2001) found that the harvestmen from the central part of N Alps were also mostly affected by elevation and light conditions. Both these works employed Canonical Correspondence Analysis (CCA; ter Braak 1987), a widely used method for direct (“constrained”) gradient analysis, that assumes species to have unimodal distributions along environmental gradients, but none of them tested if this crucial assumption of CCA was met by the data. Consequently, the interpretations may be influenced by potential non-unimodal species responses. Nevertheless, these works may be regarded as first attempts to put the relationships between harvestmen and their habitat on an objective basis. In view of these considerations, the present work will aim at contributing further to the knowledge of autoecological features of the opilionid species from the Vitosha Mountains (the region in Bulgaria with the most fully studied opilionid assemblages; see Mitov 2000) by direct modelling the response of each species towards an array of environmental factors.

Utilizing an extensive data set from a large-scale sampling program, we will focus on: 1)

summarizing the main environmental variation across the sampling localities, 2) directly modelling the response of every collected harvestmen species to the summarized multivariate gradient by using the power and flexibility of Generalised Additive Models (GAM), 3) classifying the observed response patterns of the opilionid species and 4) comparing the ecological profiles (obtained in the previous modelling stage) with published ecological data.

## METHODS

**Material collected.**—The present study is based on the examination of 31,639 specimens (8,314 males, 14,861 females, 8,464 juveniles) from 22 species and subspecies (see the number of each species caught in legend of Fig. 3), collected by the senior author in the period 28 February 1987–28 April 1989 in the region of Vitosha Mountain (peak Cherni Vrah: UTM FN81, N 42°33′48.9″, E 23°16′45.2″, 2290 m). Four species recorded from the area of the mountain (Staręga 1976; Mitov 2000; Stoyanov & Mitov 2004) are not included in the present analysis. These are: *Dicranolasma scabrum* (Herbst 1799), *Histiocostoma drenskii* Kratochvíl 1958, *Opilio parietinus* (De Geer 1778), and *Rafalskia olympica* (Kulczyński 1903). The former three species were absent from pitfall trap samples or were represented by only a few ( $n < 10$ ) individuals, while the latter species has not been recorded from Vitosha Mountain since the original record of Staręga (1976). The collected material is in the opilionid collection of Plamen Mitov.

**Sampling.**—Altogether 653 pitfall traps (plastic buckets with rim diameter 10 cm and 12 cm height), filled with 4% formalin solution were used. The traps were placed 5 m apart, on a zig-zag line through 54 sampling localities, at elevations between 750 and 2290 m (the latter is the maximum elevation for this dome-like mountain), and at intervals between 200 and 500 m (depending on the relief). All major habitat types (approximately 40% of the habitats, according to Dr. Rosen Tsonev, pers. comm.) were sampled during the sampling program that covered the whole area (278 km<sup>2</sup>) of Vitosha Mountain. Samples were collected monthly. For further details on the sampling scheme see Mitov (1996).

**Environmental data.**—At each sampling

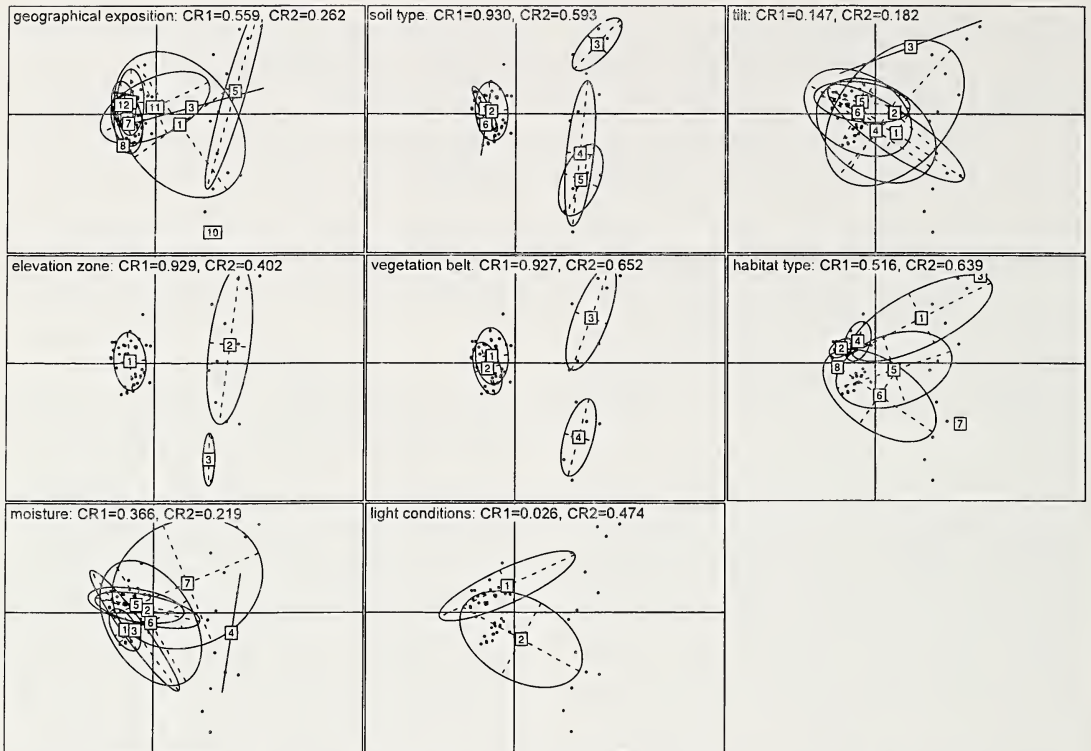


Figure 1.—Ordination diagram of the Multiple Correspondence Analysis (MCA) of the full habitat by environmental variables matrix. The first axis summarizes 11.6%, the second = 9.0% of the variability. Dots represent the sampling localities; ellipses visualize the spread of environmental variable modalities, CR1 and CR2 are the correlation ratios of each variable related to the first and second ordination axis.

locality the following environmental variables were measured and recorded (see Table 1): elevational (climatic) zone (3 classes, ordered; classification in Hubenov 1990), geographical exposition (12 classes, ordered) measured with compass, habitat type (8 classes), humidity (7 classes, ordered; based on indicator plants according to Nedyalkov 1998), light conditions (2 classes, ordered; based on habitat type), vegetation belt (4 classes; classification in Hubenov 1990), soil type (6 classes; classification in Chucheva 1983), and tilt (6 classes, ordered; classification in Chucheva 1983) measured with a standard plastic angle meter.

**Data analyses.**—The following procedure was used for modelling: 1) a Multiple Correspondence Analysis (MCA, Tenenhaus & Young 1985) was performed on the localities by environmental variables matrix to obtain a low-dimensional representation of the data structure; 2) the resulting sample ordi-

nation space (2 retained axes) was overlaid with the fitted Generalized Additive Model (GAM) surface of opilionid species abundance at the ordinated sampling sites, where the poisson error distribution and logarithmic “link function” were used for fitting. The advantage of using GAMs for the modelling is, that it is especially powerful in modelling data with non-normal error distributions (Hastie & Tibshirani 1990; Wood 2000), and that one does not have to assume a particular (unimodal or linear) response of species abundance along the environmental gradient, and thus the exploratory phase of the investigation is more flexible.

As only 9 harvestmen species were more widespread through the area of Vitosha Mountain, after modelling their abundance the site by environmental variables matrix was reduced to increase the resolution when modelling the data for the rest of the opilionid species. Fourteen high-mountain sites (in the



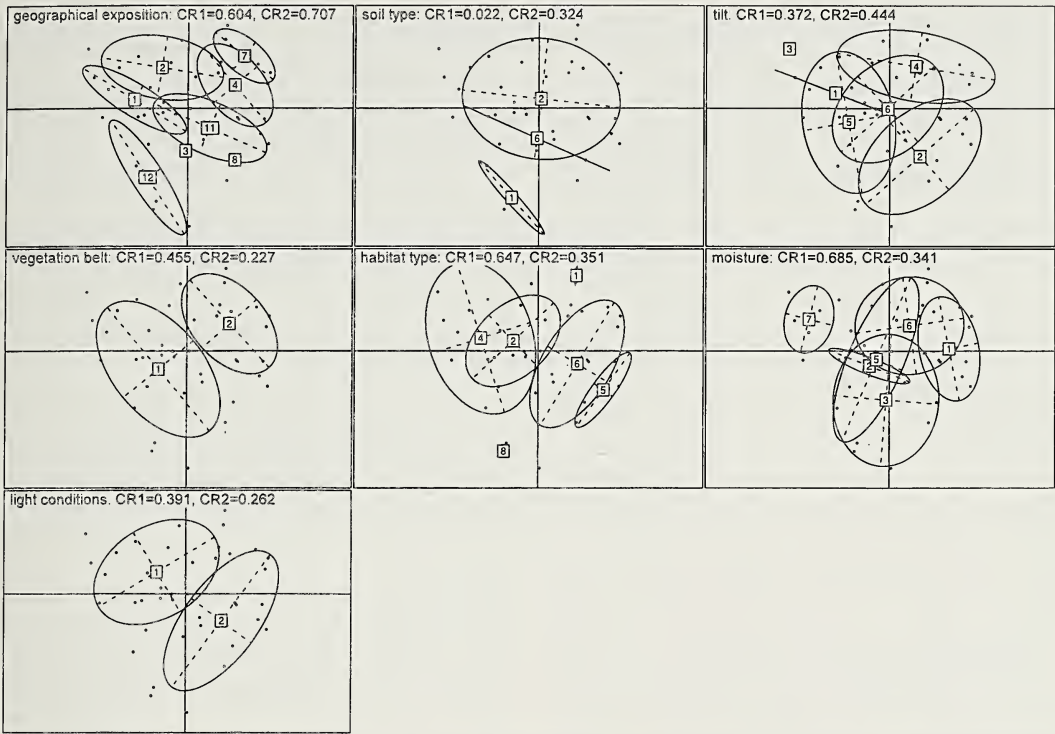


Figure 2.—Ordination diagram of the Multiple Correspondence Analysis (MCA) of the reduced habitat by environmental variables matrix (the high-mountain sites excluded). The first axis summarizes 12.2%, the second = 10.2% of the variability. Dots represent the sampling localities. For the environmental variable modalities see Table 1, ellipses visualize the spread of environmental variable modalities, CR1 and CR2 are the correlation ratios of each variable related to the first and second ordination axis.

right half of Fig. 1) were removed, in order to exclude the sites where the rest of opilionid species (13) were not (or only occasionally) present. The resulting matrix (Fig. 2) was again subjected to MCA to obtain the sampling site ordination, over which the GAM surface-fitting procedure for the remaining (i.e. those restricted to the low-mountain zone) species was applied again. All computations were performed in the R statistical language and environment (Ihaka & Gentleman 1996), using the *ade4* (Chessel et al. 2004), *mgcv* (Wood 2000), and *akima* (Akima 1978) libraries.

RESULTS

**Environmental gradients.**—The MCA on the sampling site by environmental variable matrix shows a strong separation of the low-mountain from the high-mountain zone (including the a priori defined middle-mountain zone, cf. “METHODS”) along the first ordi-

nation axis (see Fig. 1, “elevational zone”). The environmental variables with high correlation ratio with this axis (and thus enabling a good separation of the sampling sites along that axis) also include soil type, vegetation belt (both presenting a structure very similar to that of the elevational zone), and exposition. Most strongly associated with the second ordination axis are the following variables: vegetation belt, habitat type, soil type, and light conditions (Fig. 1). The similar patterns of soil type, elevational zone and vegetation belt are due to strong interdependence between these factors.

When analyzing the reduced sites by environmental variables matrix (Fig. 2), a not so abrupt (and hence more complex) gradient is apparent. Its first axis is mainly determined by the moisture gradient, the habitat type, and exposition, while the exposition, tilt, habitat and moisture (both similarly important) summarize the main variation along the second or-

Table 1.—Environmental variables measured at each sampling locality.

Variable	Classes
Elevational zone	1) low- (up to 1450 m), 2) middle- (1450–1850 m), 3) high-mountain zone (above 1850 m, max. 2290 m)
Geographical exposition	1) N, 2) NNE, 3) NE, 4) ENE, 5) E, 6) SE, 7) SSE, 8) S, 9) SW, 10) WSW, 11) W, 12) NNW
Habitat type	1) coniferous forests, 2) deciduous forests, 3) rivulet-bank in coniferous forests, 4) rivulet-bank in deciduous forests, 5) rivulet-bank through meadows, 6) meadows, 7) peat moss bogs, 8) forest-glades
Humidity	1) dry, 2) dry-mesophilous, 3) dry-fresh, 4) mesophilous-fresh, 5) fresh, 6) fresh-moist, 7) moist
Light conditions	1) dark, 2) light
Vegetation belt	1) <i>Quercus-Carpinus</i> , 2) <i>Fagus</i> , 3) coniferous, 4) subalpine
Soil type	1) Chromic Luvisols, 2) Distric Cambisols, 3) Humic Cambisols, 4) Orthic Umbrosols, 5) Rendzic Leptosols, 6) Histic Umbrosols
Tilt	1) 0–5°, 2) 6–10°, 3) 11–20°, 4) 21–30°, 5) 31–40°, 6) 41–50°

dination axis (see the correlation ratios in Fig. 2).

**Modelled ecological profiles.**—As evident from the distribution plots (Fig. 3), the distribution-patterns of the Opiliones from Vitosha Mountain may be classified in two groups. The first one contains species with region-wide distribution (indicated by the spread of lines that connect the sampling sites where a species has been sampled): *Pyza bosnica* (Roewer 1919), *Paranemastoma radewi* (Roewer 1926), *Paranemastoma aurigerum ryla* (Roewer 1951), *Phalangium opilio* Linnaeus 1758, *Rilaena* cf. *serbica* Karaman 1992, *Lophopilio palpinalis* (Herbst 1799), *Lacinius horridus* (Panzer 1794), *Mitopus morio* (Fabricius 1779), and *Leiobunum rumelicum* Šilhavý 1965. The second group include opilionid species restricted more or less to the low-mountain zone (the compact cluster, located left of the main vertical axis on Fig. 3). These are *Mitostoma chrysomelas* (Hermann 1804), *Carinostoma ornatum* (Hadži 1940), *Trogulus tricarinatus* (Linnaeus 1767), *T. closanicus* Avram 1971, *Opilio saxatilis* C. L. Koch 1839, *O. ruzickai* Šilhavý 1938, *O. dinaricus* Šilhavý 1938, *Rilaena balcanica* Šilhavý 1965, *Zachaeus crista* (Brullé 1832), *Z. anaticus* (Kulczyński, 1903), *Lacinius dentiger* (C.L. Koch 1847), *L. ephippiatus* (C.L. Koch 1835), *Odiellus lendli* (Sørensen 1894).

The fitted GAM surfaces for some of the members of the first group mentioned above do not show any prominent optimum within the study area, as for example *Pyza bosnica*,

*Paranemastoma radewi*, *Lophopilio palpinalis*, and *Mitopus morio* (Fig. 4). These species increase their abundance towards the margin of the scatterplot more or less linearly. The first mentioned species has its maximum abundance in the low-mountain zone as well as in the coniferous forest habitats (in the middle-mountain zone); the second species tends to occur more massively in deciduous forests (in the low-mountain zone), and the latter two reach highest numbers in the middle- and high-mountain zones respectively. *Leiobunum rumelicum* is mainly distributed in forest habitats (predominantly in the low-mountain zone and several occupied localities in the middle-mountain zone). *Rilaena* cf. *serbica* and *Phalangium opilio* seem to prefer middle-mountain open habitats (where a well defined peak may be observed); a similar pattern is also displayed by *Paranemastoma aurigerum ryla*, but the peak is not so prominent. Finally *Lacinius horridus* shows a clearly bimodal distribution pattern, showing a prominent peak in forests of the low-mountain zone and increasing at the same time its abundance towards open habitats in the middle-mountain zone.

From the predominantly low-mountain harvestmen species, *Zachaeus crista* (Fig. 5) and *Trogulus tricarinatus* (not shown) are more or less evenly distributed within the zone. *Rilaena balcanica* (Fig. 5), *O. dinaricus*, and *Opilio ruzickai* (both not shown) are clearly associated with forests locations in the oak-hornbeam vegetation zone. The modelled responses of *Carinostoma ornatum* and *Opilio*



*saxatilis* (Fig. 5) show a clear preferendum (peak) towards relatively dry and open habitats, the peak of the latter species is more towards open and dryer (and not so slanted) stations (cf. the habitat characteristics distribution on Fig. 2).

In contrast to the previously mentioned species, the following harvestmen do not show a pronounced optimum in their response. *Lacinius dentiger* (Fig. 5) and *Lacinius ephippiatus* (not shown) demonstrate a slightly bimodal response, being strongly associated with fresh to moist slanted forest habitats in both the beech and oak-hornbeam vegetation belt (the latter species being more dependent on moisture conditions, than the former). A somewhat bimodal, but not easy interpretable response pattern may be observed on the GAM plot for *Trogulus closanicus* (Fig. 5). This species seems to be associated with fresh to moist riverside habitats in forests and fresh meadows, but due to the relatively low number of individuals collected, this pattern is not very well supported.

Finally, the abundances of three of the opilionid species: *Mitostoma chrysomelas*, *Zachaeus anatolicus* and *Odiellus lendli*, could not be modelled because of their very restricted occurrence (i.e. very low frequency and abundance of catches) on Vitosha Mountain. The last mentioned species were collected mainly on a few meadows, and while *Z. anatolicus* could be regarded as relatively rare throughout Bulgaria, *O. lendli* was locally very abundant (911 specimens come from a fresh beech forest meadow).

When focusing on the response types of congeneric opilionid species, we may observe that these species tend to display opposite trends, as for example the species of the genera *Paranemastoma* Redikorzev, 1936 (Figs. 3, 4), *Lacinius* Thorell, 1876 and *Rilaena* Šilhavý 1965. The differences are not so prominent in the responses of the *Trogulus* Latreille 1802 and *Zachaeus* C.L. Koch, 1839 species, while in species of the genus *Opilio* Herbst, 1798 only the response of *O. saxatilis* shows a trend opposite to the responses of the other species from this genus (Fig. 3).

**Ecological profiles from literature data.**—When examining the published ecological profiles of harvestmen species, four groups can be delimited.

1. In the first one we include species that

have repeatedly been reported to prefer moist habitats in forests. These are *Paranemastoma radewi* (Staręga 1976; Mitov 1986, 1996), *Pyza bosnica* (Staręga 1976; Mitov & Stoyanov 2004), *Paranemastoma aurigerum* ryla (see Staręga 1976), *Lophopilio palpalis* (Pfeifer 1956; Cîrdei & Bulimar 1960; Hiebsch 1972; Weiss 1975; Staręga 1976; Martens 1978; Geyer 1983; Bliss & Tietze 1984; Müller 1984; Platen et al. 1991; Platen 1996, 2000; Platen & Broen 2002; Komposch 1997a, b, 1999; Metzen & Cölln 1998; Komposch & Gruber 2004; Mitov & Stoyanov 2004; but see above for alternative opinions) and *L. ephippiatus* (Mitov & Stoyanov 2004). Nevertheless, many European harvestmen researchers have described the latter as eurytopic (Platen et al. 1991; Platen 1996, 2000; Platen & Broen 2002; Komposch 1997a, 1999), hygrophilous (Martens 1978; Hiebsch 1978; Müller 1984; Platen et al. 1991; Karaman 1995; Komposch 1997a, 1999, 2001; Komposch & Gruber 2004), thermophilous (Pfeifer 1956), or as a montane forest species (Staręga 1976). Despite the scarce information in the literature about the ecological status of *Leio- bunum rumelicum*, which only Staręga (1976) reported as a species inhabiting montane forests, we add this species to the above mentioned group.

2. According to the examined literature sources, most of the species found in the Vitosha Mountain seem to generally prefer thermophilous forests in the low-mountain zone. This group include *Rilaena* cf. *serbica* (only recently reported from Bulgaria by Mitov & Stoyanov 2004 who described it as thermophilous forest-dweller), *Lacinius horridus* (Pfeifer 1956; Staręga 1976; Martens 1978; Thaler 1979; Müller 1984; Platen et al. 1991; Weiss 1996; Karaman 1995; Metzen & Cölln 1998; Komposch 1999; Platen & Broen 2002; Komposch & Gruber 2004; Mitov & Stoyanov 2004), and *Trogulus tricarlinatus* (Kolosváry 1965; Staręga 1976; Martens 1978; Platen et al. 1991; Karaman 1995; Weiss 1996; Komposch 1997a, 1999; Metzen & Cölln 1998; Platen 2000; Muster 2001; Platen & Broen 2002; Komposch & Gruber 2004; Mitov & Stoyanov 2004; but Komposch & Gruber (2004) question its thermophily). As the representatives of genus *Zachaeus* C.L. Koch 1839 have been repeatedly classified as thermophilous (Martens 1978), it is understand-

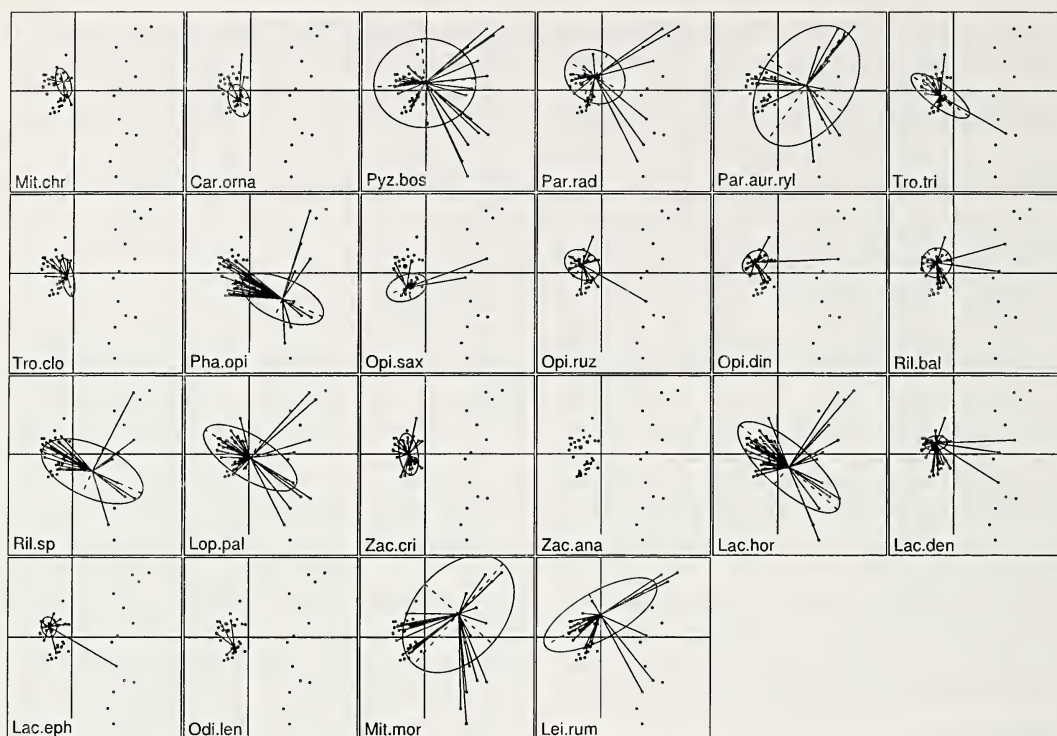


Figure 3.—Distribution plot of the Opiliones from Vitosha Mountain. The space of sampling localities (dots) is the same as in Fig. 1; lines connect samples where each species is present with the centroid of the distribution; ellipses visualize the spread of individual species occurrences. Species name abbreviations: Mit.chr (*Mitostoma chrysomelas*,  $n = 17$  sampled individuals), Car.orna (*Carinostoma ornatum*,  $n = 45$ ), Pyz.bos (*Pyza bosnica*,  $n = 1844$ ), Par.rad (*Paranemastoma radewi*,  $n = 774$ ), Par.aur.ryl (*P.aurigerum ryla*,  $n = 318$ ), Tro.tri (*Trogulus tricarinatus*,  $n = 89$ ), Tro.clo (*T. closanicus*,  $n = 155$ ), Pha.opi (*Phalangium opilio*,  $n = 2875$ ), Opi.sax (*Opilio saxatilis*,  $n = 103$ ), Opi.ruz (*O. ruzickai*,  $n = 76$ ), Opi.din (*O. dinaricus*,  $n = 318$ ), Ril.bal (*Rilaena balcanica*,  $n = 996$ ), Ril.sp (*R. cf. serbica*,  $n = 533$ ), Lop.pal (*Lophopilio palpalis*,  $n = 1881$ ), Zac.cri (*Zachaeus crista*,  $n = 1431$ ), Zac.ana (*Z. anatolicus*,  $n = 26$ ), Lac.hor (*Lacinius horridus*,  $n = 12164$ ), Lac.den (*L. dentiger*,  $n = 1950$ ), Lac.eph (*L. ephippiatus*,  $n = 689$ ), Odi.len (*Odiellus lendli*,  $n = 1002$ ), Mit.mor (*Mitopus morio*,  $n = 4021$ ), Lei.rum (*Leiobunum rumelicum*,  $n = 342$ ).

able that *Zachaeus crista* also falls into this group (Starega 1976; Weiss & Sârbu 1977; Martens 1978; Weiss 1975, 1996; Karaman 1995; Mitov 2003; Mitov & Stoyanov 2004). Here we include also *Opilio ruzickai* (Starega 1976; Komposch & Gruber 2004; Mitov & Stoyanov 2004), *Opilio dinaricus* (Komposch 1997a, 1999; Mitov & Stoyanov 2004), *Rilaena balcanica* (Starega 1976; Mitov & Stoyanov 2004) and *Lacinius dentiger* (Cîrdei & Bulimar 1960; Starega 1976; Martens 1978; Thaler 1979; Karaman 1995; Komposch 1995, 1997a, 1999; Platen & Broen 2002; Komposch & Gruber 2004; Mitov & Stoyanov 2004).

3. The third group includes harvestmen that occur in forests, as well as in open habitats.

These species have been frequently described as eurytopic, such as *Mitopus morio* (e. g. Cîrdei & Bulimar 1960; Tischler 1967; Starega 1976; Martens 1978; Geyer 1983; Müller 1984; Platen et al. 1991; Karaman 1995; Komposch 1997a,b, 1999; Metzen & Cölln 1998; Zingerle 1999, 2000; Platen 2000; Muster 2001; Platen & Broen 2002; Komposch & Gruber 2004), *Mitostoma chrysomelas* (Martens 1978; Weiss 1984, 1996; Karaman 1995; Komposch 1997a,b; Metzen & Cölln 1998; Zingerle 1999, 2000; Muster 2001; Komposch & Gruber 2004); the latter has also been described as euryphotic-hygrophilous (Hiebsch 1972) and forest hygrobiont/philic species, also inhabiting open habitats (Meijer 1972; Starega 1976; Platen et al. 1991; Platen 1996,



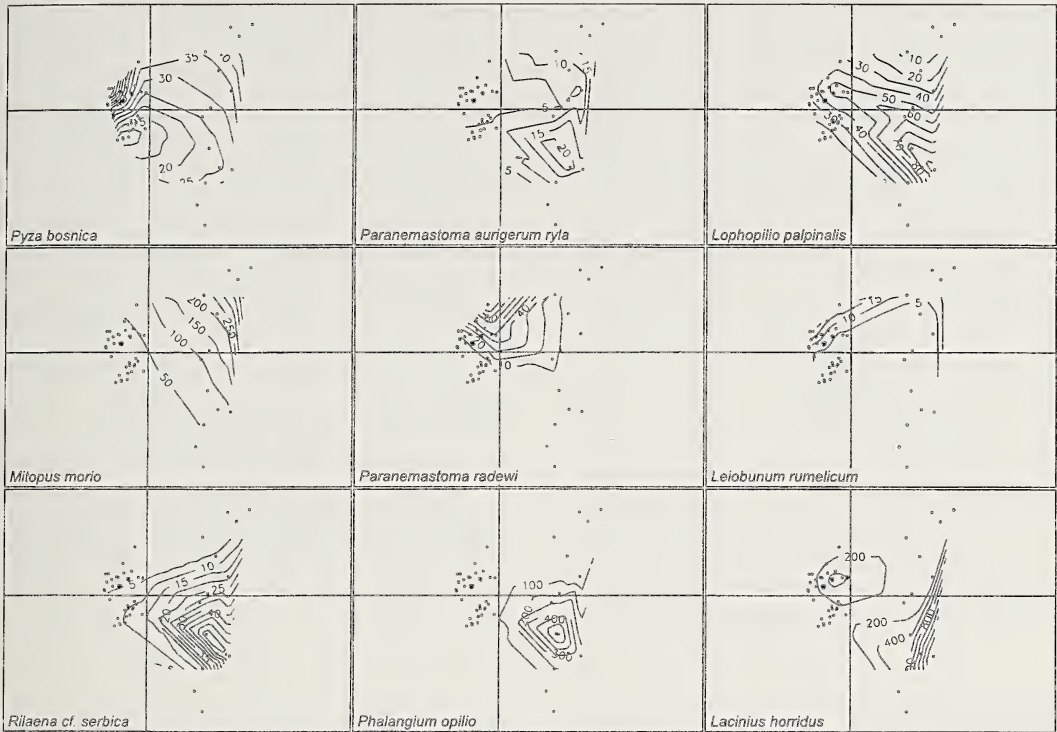


Figure 4.—GAM surface plots for the modelled abundance of harvestman species that occurred at all elevations: *Pyza bosnica*, *Paranemastoma aurigerum ryla*, *Lophopilio palpinalis*, *Mitopus morio*, *Paranemastoma radewi*, *Leiobunum rumelicum*, *Rilaena cf. serbica*, *Phalangium opilio*, *Lacinius horridus*. The space of sampling localities (dots) is the same as in Fig. 1; the isolines show the modelled abundance of each species.

2000; Platen & Broen 2002). *Carinostoma ornatum* (Staręga 1976; Mitov 1986; Karaman 1995; Mitov & Stoyanov 2004), *Trogulus clo-sanicus* (Weiss 1978, 1996; Komposch 1997a, 1999; Metzen & Cölln 1998; Mitov & Stoyanov 2004) and the thermophilous, photophilous and xerophilous *Odiellus lendli* (Staręga 1976; Weiss & Sârbu 1977; Mitov & Stoyanov 2004) are also included in this group.

4. The last three species may be listed together as harvestmen characteristic of open habitats. This group contains the relatively well known, ecologically widely adapted, photophilous, and thermophilous species such as *Phalangium opilio* and *Opilio saxatilis* (Pfeifer 1956; Kolosváry 1965, 1966a,b; Staręga 1976; Weiss & Sârbu 1977; Hiebsch 1978; Czechowski et al. 1981; Klimeš 1987; Kuschka 1991; Platen et al. 1991; Platen & Broen 2002; Karaman 1995; Weiss 1996; Komposch 1997a, 1999, 2001, 2004; Metzen & Cölln 1998; Mitov 2003; Komposch & Gruber 2004; Mitov & Stoyanov 2004), as

well as *Zachaeus anaticus*, a Balkan sub-endemic (Mitov 2004), that may also be included here, based on a single report about its thermophilic nature (Mitov 2001).

DISCUSSION

According to the summarized literature data, habitat type and moisture are the most important factors for the ecological classification of the opiloid species. Our data, gathered from a study at a Bulgarian mountain, demonstrated that the main factor responsible for determining the ecological profiles of the harvestmen is elevation. But since elevation could not be regarded as a physiologically active factor *per se*, it may be suggested that elevational biotic (e.g. the decrease of productivity) or abiotic (e.g. low amount of available microhabitats, harsher climatic conditions) correlates, or even an unmeasured environmental parameter, would rather be the immediate ecological component acting upon the harvestmen. However, the habitat type and

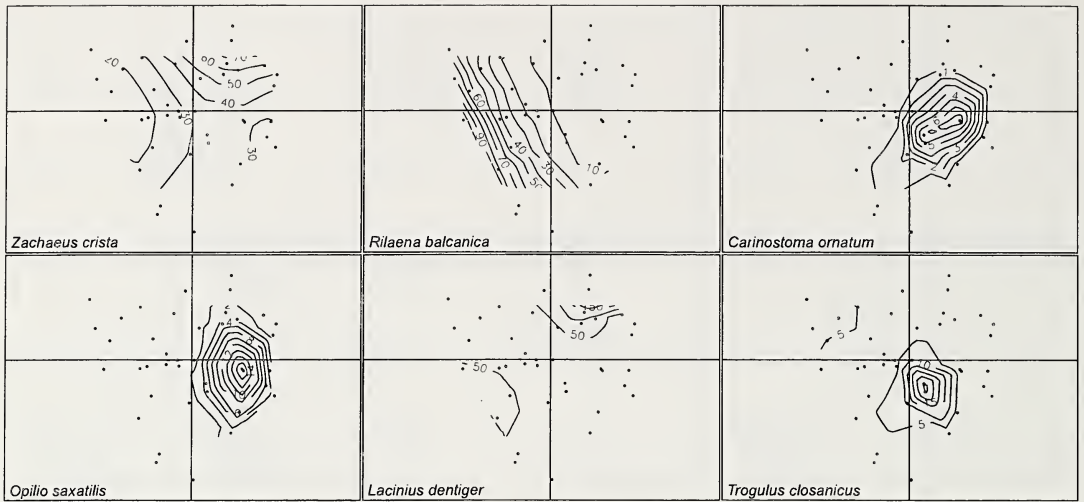


Figure 5.—GAM surface plots for the modelled abundance of harvestman species that occurred only at low-elevations localities: *Zachaeus crista*, *Rilaena balcanica*, *Carinostoma ornatum*, *Opilio saxatilis*, *Lacinius dentiger*, *Trogulus closanicus*. The space of sampling localities (dots) is the same as in Fig. 2; the isolines show the modelled abundance of each species.

moisture turned out to be of some importance for the species in the low-mountain zone of Vitosha, mainly because the habitat type depends on moisture on one hand and regulates it on the other. This observation is in concordance with the observations of Platen (pers. comm.) that in Germany most harvestmen species occur in shady and somewhat moist habitats. It might be suggested that elevation was found to be an important factor mainly because of the “mountainous” character of this study, but two further works, one on a mountain (Muster 2001; Alps) and a region-wide one (Klimeš 1997, data from the entire Czech Republic) also demonstrated the primary role of elevation for shaping the opilionid assemblages.

One particular reason for the failure of this investigation to show any strong association of the Opiliones with factors other than elevation, could be a result of the very complex environmental matrix obtained in this study. The habitat parameter that showed the best spread among the sampled localities was the elevation (and its correlates such as vegetation belt and soil type; see Figs. 1, 2). The other measured environmental parameters do not show such a broad variation among sampling units, and thus may not contribute significantly to their discrimination. Consequently, when modelled over the ordination plane, the

response of individual species could not be clearly associated with environmental factors that do not demonstrate large variation across the investigated area, especially when these responses do not show any pronounced optima at factor centroids. Another reason could be the dependence of harvestmen on various structures or conditions occurring within a specific habitat (and not on the habitat itself). Since we have not investigated microhabitat structures, this question should remain open until a study focused on within-habitat (microhabitat) structures is conducted.

In contrast to the mostly unnuanced and undiversified classifications found in the literature, is the finding that different species show quite different response-types towards the environmental parameters. This fact could not be discovered by the modelling studies cited above (Klimeš 1997; Muster 2001), since these have employed the modelling technique of choice without verifying its basic assumptions (i. e. the unimodal response of species). We found that in fact the minority of the harvestmen species from Vitosha Mountain had a unimodal distribution with a clear optimum (or preferendum) throughout the studied area. This linear response may be due to the investigations following a gradient of elevation, and because some species have made their niche at a certain elevation to avoid compe-



tition and/or unfavourable environmental conditions. As Platen pointed out (pers. comm.), even in a lowland opilionids may display unimodal responses along gradients of moisture and light exposure, respectively. Whether there is a bimodal response in some species can be precisely decided in laboratory experiments, but it may be suggested that it would be of rare occurrence in Opiliones because of their strong dependence on humidity. In this situation it may be argued that an even more variable environmental matrix (i.e. with broader amplitude of environmental conditions, or including more measured environmental variables) and/or specially designed laboratory experiments should be used for refining the delineated ecological profiles, as well as for allowing the observation of potential uni- and bimodal responses of harvestmen species.

Another important information that emerged from this study is that congeneric species are quite different in their responses towards the environmental variables. This has been repeatedly postulated by theoretical ecologists as a mechanism for minimizing the potential competition (e.g. Begon et al. 1996; Giller 1984), and we suggest that this could be valid also for the Opiliones from Vitosha Mountain.

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## INFLUENCE OF GRAZING BY LARGE MAMMALS ON THE SPIDER COMMUNITY OF A KENYAN SAVANNA BIOME

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**ABSTRACT.** Pitfall trap and sweep net samples were taken over a period of fifteen months (2002–2003) in the Kenya Long-term Exclosure Experiment (KLEE), in which the presence of domestic and wild herbivores have been independently manipulated since 1995. ANOVA and ANCOVA showed that the exclosure treatments significantly affected plant cover, with the presence of cattle significantly reducing the relative vegetation cover and spider diversity. Herbivory by indigenous mega- and meso-herbivores did not have a significant influence on the diversity of the spider fauna, but abundance of three dominant species (*Cyclosa insulana* Costa (Araneidae), *Argiope trifasciata* Forskål (Araneidae) and *Runcinia flavida* Simon (Thomisidae)) decreased in cattle-grazed plots. In contrast, *Aelurillus* sp. became more prevalent where cattle have been grazing. Multivariate analyses revealed that the spider community responded to grazing pressure by aggregating into three groups that reflected control, cattle grazing and non-cattle grazing clusters. It was probable that the direct effects on vegetation mediated an indirect influence of herbivores on spider diversity. The relative vegetation cover was a positive predictor of spider diversity. Spider communities were found to be an indicator of the activity of mammals and could be used as indicators of land use changes and for bio-monitoring.

**Keywords:** Grazing, mammals, savanna, Kenya, spiders

**Savanna inventories.**—Little ecological work has been done on spiders of African savannas and inventories from this habitat are rare. For example, the only inventory work in Kenya was carried out by Russell-Smith et al. (1987), who reported 68 species from Kora Game Reserve. Recently, Warui et al. (2004) reported a checklist of 132 species from a black cotton soil ecosystem in Laikipia. In Tanzania, a checklist of 508 species from Mkomazi Game Reserve was published by Russell-Smith (1999). In South Africa, several surveys of spiders were undertaken in the Savanna Biome. Dippenaar-Schoeman et al. (1989) reported 98 species from Rooideplaas Dam Nature Reserve while Dippenaar-Schoeman and Leroy (2003) reported another 152 species from the Kruger National Park and Foord et al. (2002) recorded 127 species from the western Soutpansberg. Another 55 species were recorded from Rietondale, Pretoria (van

den Berg & Dippenaar-Schoeman 1991), and 268 species from Makalali Game Reserve in the Limpopo Province (Whitmore et al. 2001). Lastly Lotz et al. (1991) working on grassland biome reported 31 families of spiders from Bloemfontein. The only other works on savanna spiders apart from check-lists are those of Russell-Smith (1981), who reported 135 species from Botswana; and Blandin & Cél-érier (1981), who studied savanna spiders in Ivory Coast.

**Current study.**—This study was part of the Kenya Long-term Exclosure Experiment (KLEE), a long-term multi-species vertebrate herbivore exclusion experiment in a semi-arid savanna ecosystem in Laikipia, Kenya (Young et al. 1998). KLEE is aimed at comparing the impacts of cattle and wildlife (elephants, giraffes, buffaloes, antelopes and other savanna ungulates) on various components of the savanna biome including biodiversity. Refer-

ence is made to spiders because they inhabit a large array of microhabitats ranging from the ground layer, to the tree layer and makes them particularly suitable to integrate and evaluate activity by the different guilds of herbivores. Since the response of spiders to the particular structure of the habitat is very fine-grained (Gunnarsson 1988; Uetz 1991; Rypstra et al. 1999), it was expected that changes caused by the different guilds of herbivores, would be reflected in the spider fauna. The influence of abiotic environmental variables was also investigated for a few individual species.

Most studies on the influence of grazing and trampling concentrate on the effects on the fauna or vegetation as a whole. Outside Africa and in different ecosystems, such general investigations were carried out by Gibson et al. (1982, 1992) and Curtis et al. (1990) who found that communities of spiders were negatively affected by grazing and trampling. Abensperg-Traun et al. (1996) studied the grazing impact of mammals on invertebrates in Australian woodland and found that the abundance of the spider families Idiopidae and Lycosidae was highest in moderately disturbed woodlands. Rambo & Faeth (1998) looked at influence of grazing on plant insect communities. In Africa, Woldu & Saleem (2000) focused on plant biodiversity in Ethiopia, while Rivers-Moore & Samways (1996), Fabricius (1997), Seymour (1998), Seymour & Dean (1999) and Fabricius et al. (2002) demonstrated that grazing or trampling has effects on various groups of invertebrates in South Africa. Earlier African studies were reviewed in Skarpe (1991). Few studies are available that report the influence of grazing on spiders in particular: Churchill (1998) reported a variation in the abundance of dominant spider families along grazing and rainfall gradients in Australian tropics. Abrous-Kherbouche et al. (1997) investigated the effects of grazing in mountain grassland in North Africa. The present study is the first that studies the subject in tropical Africa and uses a large-scale experimental set-up for the purpose. This is the second paper on Kenyan savanna spiders by the author and more reference can be made to Warui et al. (2004).

#### METHODS

**Study area.**—The study was conducted at Mpala Research Centre (MRC) (00°17'N

037°52'E, 1750–1800 m asl), a 1200 ha piece of land adjacent to Mpala Ranch in the Laikipia District of central Kenya. The study site is characterized by black cotton soil (Chromic vertisols), which are heavily textured cracking clays with impeded drainage (Ahn & Geiger 1987; Taiti 1992). Its vegetation is Acacia bushed grassland (Young et al. 1998) dominated by *A. drepanolobium* (Harms) Sjøstedt, accounting for over 95% of the woody vegetation. Rainfall averages 500–600 mm per year (Young et al. 1995, 1998). Data were collected from May 2001 to July 2002.

**The KLEE study design.**—The Kenya Long-term Exclosure Experiment is a set up in which the presence of domestic and wild herbivores has been independently manipulated since 1995. KLEE allows herbivory (grazing and browsing) in six combinations of three categories of herbivores. These three categories are (1) meso-wildlife (W) (or meso-herbivores: buffalo and other smaller ungulates), referred to as 'wildlife' in Young et al. (1998); (2) mega-wildlife (M) (or mega-herbivores: giraffes and elephants); and (3) cattle (C). The grazing by cattle was moderate, with one livestock unit per 5–8 ha (Young et al. 1998). The details of this design are shown in Fig. 1. The three categories of the large mammalian herbivores were managed such that (i) only cattle (C); (ii) only meso-herbivores (W); (iii) only mega-herbivores and meso-herbivores (MW); (iv) mega-herbivores, meso-herbivores and cattle (MWC); (v) only meso-herbivores and cattle (WC); and (vi) no large mammalian herbivores (control, O) were allowed to graze/browse. Each treatment plot is 200 × 200 m and is replicated three times, once in each of three blocks (north, central and south), totaling 18 plots.

**Spider collection.**—Spiders were collected with pitfall traps and by sweep-netting. Much has been published about advantages and limitations of pitfall traps (e.g., Greenslade 1964; Uetz & Unzicker 1976; Spence & Niemelä 1994; Green 1999; New 1999) and this study employed them to allow comparison with data from published studies. The pitfall traps consisted of two cone-shaped plastic (polyethylene) cups 9 cm wide at the mouth and 14 cm deep, one inside the other, buried to their rim. Three pitfalls per plot for each of the 18 sampling plots were used, making a total of 54 traps. The three pitfall traps were laid on a



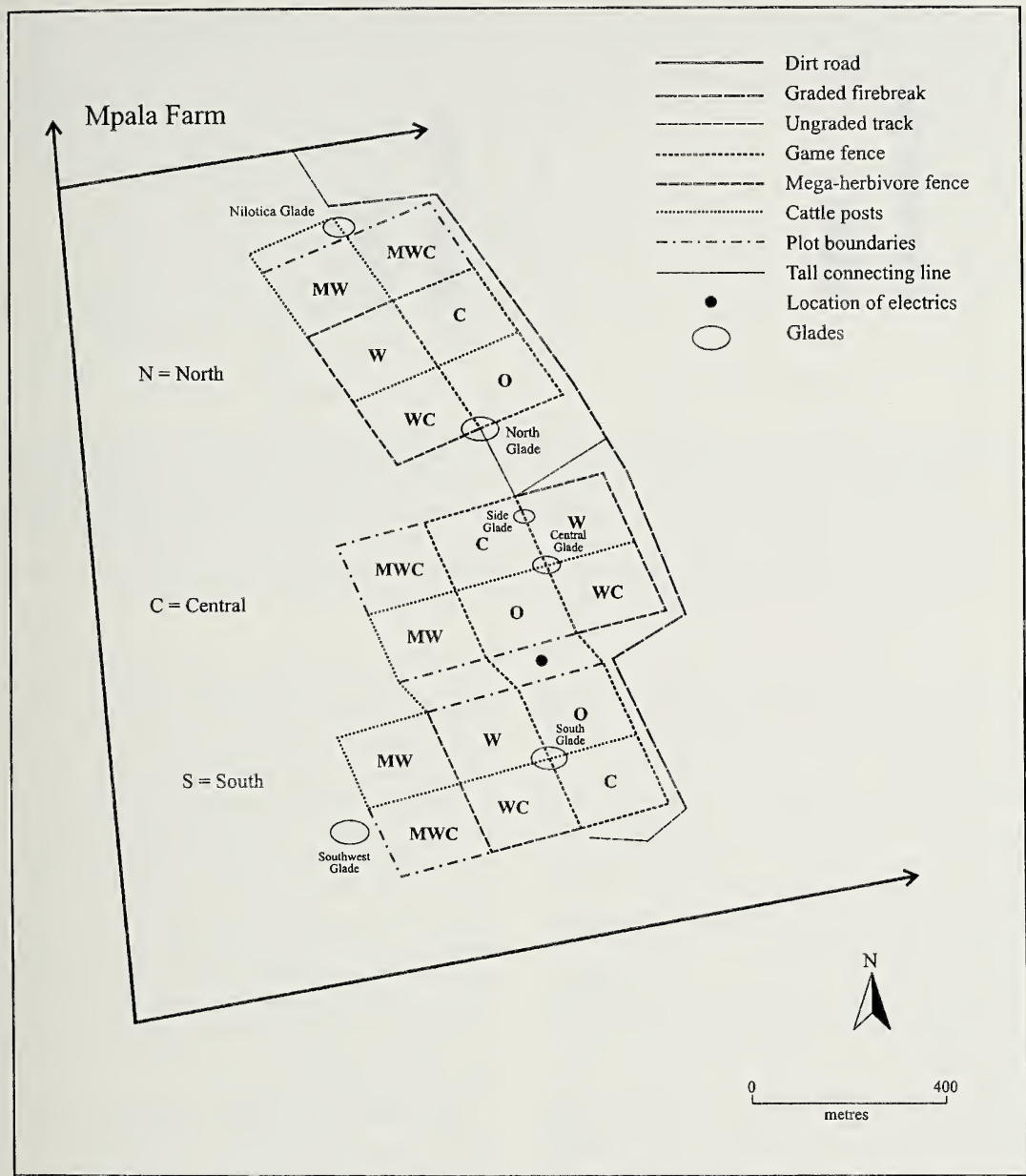
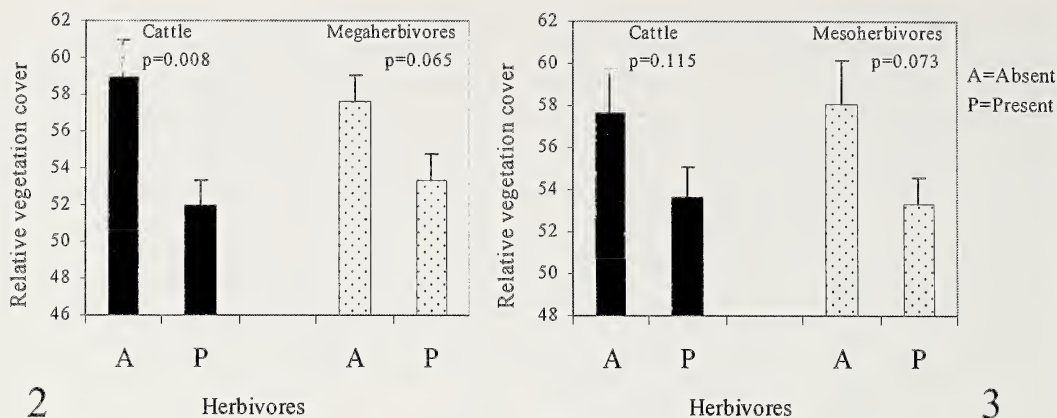


Figure 1.—Schematic representation of the experimental design of the KLEE study plots at Laikipia, Kenya. Letters in each plot represent the herbivores allowed in: C = cattle, W = meso-herbivores, M = mega-herbivores, O = control (all large mammalian herbivores excluded). N, C and S represent north, central and south blocks respectively. Each plot measures 200 × 200 m. The distance between the furthest placed plots (between north and south block) is approximately 2 km. Adapted from Young et al. (1998).

line transect every 3 m. The inner cup of each trap was filled to a third of its volume with a 2% formaldehyde solution as a preservative. Traps were left open and emptied every second week. Sweep-netting was done by walking through the herb layer swinging a sweep

net (40 cm in diameter) through the vegetation for a standard number of times (Coddington et al. 1996; Scharff & Griswold 1996; Dippenaar-Schoeman et al. 1999). Sweeping was done on a randomly selected 50 m transect in each of the 18 plots. A hundred sweeps (emp-



Figures 2–3.—2. Effects of 'cattle' (levels: absent [treatments W and MW] vs. present [WC and MWC]) and 'megaherbivores' (levels: absent [W and WC] vs. present [MW and MWC]) on relative vegetation cover (mean ± SE). Two treatments (O and C) were omitted from the data set so that the analysis was fully crossed. The interaction term was not significant ( $P = 0.28$ ). 3. Effects of 'cattle' (levels: absent [O and W] vs. present [C and WC]) and 'mesoherbivores' (levels: absent [O and C] vs. present [W and WC]) on relative vegetation cover (mean ± SE). Two treatments (MW and MWC) were omitted from the data set so that the analysis was fully crossed. The interaction term was not significant ( $P = 0.79$ ).

tied after every 10 sweeps with an aspirator) were made along each transect. The process was repeated every fortnight throughout the study period.

**Vegetation sampling.**—The vegetation cover was sampled once every month in all the study plots using a ten-point pin frame and quadrat methods where samples were collected on sweep-netting and pitfall-trapping transects. The percentage relative vegetation cover was calculated by deducting the total number of bare hits from pin totals to give the plant cover hits, which were then expressed as a percentage.

**Weather measurements.**—Monthly rainfall was recorded using three rain gauges placed in each of the three study blocks (north, central and south). The mean maximum temperature is between 24 and 27 °C (Ahn & Geiger 1987).

**Statistical analyses.**—Four diversity indices [Shannon-Wiener (H), Margalef (d), Pielou (J) and total species (S)] were computed using PRIMER (Clarke & Gorley 2001). Other statistical tests were performed using STATISTICA (StatSoft 1999). In this study, ordinations by non-metric multidimensional scaling (MDS) were computed in the MDS module of PRIMER, where the original abundance data matrix was first converted into a Bray-Curtis similarity matrix using the SIM-

PLER module of PRIMER (Clarke & Warwick 1994). This is the most commonly used similarity coefficient in ecological work and accounts well for rare species. It down-weights the contributions of rare species in an entirely natural way such that the rarer the species, the less it contributes (Clarke & Warwick 1994). MDS only considers that an ordination is a reasonable representation of similarity by looking at stress values which range from 0-1 and increase with reduced dimensionality of the ordination. Low stress values (< 0.1) are the best two-dimensional presentation of data points. In the current study only ten iterations were used.

**Normality and transformation of data.**—Levene's test was used to test the homoscedasticity of the data while data on percentage relative vegetation cover were arcsine-transformed before being subjected to ANOVA. Square root transformation was performed on all spider abundance data in order to make the underlying distribution normal before any ANOVA or analyses of covariance (ANCOVA) were performed. ANOVA and ANCOVA results were done only where Levene's test was not significant or there were no serious violation of the assumptions of ANOVA.

## RESULTS

A total of 10,487 specimens, representing 132 species in 30 families, were collected



Table 1.—Results of ANOVA on effects of the factors ‘cattle’ (levels: absent [treatments O, W and MW] vs. present [C, WC and MWC]) and ‘herbivores’ (levels: herbivores absent [O and C], only meso-herbivores present [W and CW], and both meso- and mega-herbivores present [MW and MWC]) on relative vegetation cover. The codes for the treatment abbreviations are (cf. Fig. 1): O = control (no large mammalian herbivores); W = meso-herbivores; M = mega-herbivores and C = cattle. No treatments were omitted from the data set. \* = Significant at  $\alpha = 0.05$ .

Factor	Mean relative cover $\pm$ SE		df	MS	F	P
	Absent	Present				
Cattle	59.24 $\pm$ 1.74	53.43 $\pm$ 1.18	1	151.90	8.77	0.012*
Herbivores	58.06 $\pm$ 2.08	57.61 $\pm$ 2.67	2	40.86	2.36	0.137
Cattle & Herbivores	56.35 $\pm$ 1.22	52.94 $\pm$ 2.60	2	14.61	0.84	0.454
Error			12	17.31		

from the study area (Warui et al. 2004). Newly recorded species appeared throughout the sampling period for both sweep-netting and pitfall (see Warui et al. 2004). The sweeping method accounted for 67 species and pitfall-trapping accounted for approximately 110 species.

**Vegetation cover.**—The first analysis used all six cattle treatments with two levels for the factor ‘cattle’ (present/absent), and three levels for the factor ‘herbivores’ (absent/only meso-herbivores present/both meso- and mega-herbivores present). Only the presence of cattle had a significant, negative effect on vegetation cover (Table 1). Similarly, a second analysis tested the effects of the factors ‘cattle’ (with levels present vs. absent) and ‘mega-herbivores’ (with levels present vs. absent), using all treatments containing herbivores (W, WC, MW, MWC). Two treatments (O and C) were omitted because the KLEE experimental layout was not fully crossed. This analysis revealed that only the presence of cattle had a significant, negative effect on vegetation cover ( $F_{1,8} = 12.31, P = 0.008$ , Fig. 2). Mega-herbivores had an almost significant negative effect on relative vegetation cover ( $F_{1,8} = 4.59, P = 0.065$ , Fig. 2). A third analysis tested the effects of the factors ‘cattle’ (with levels present vs. absent) and ‘meso-herbivores’ (with levels present vs. absent) in the four treatments that excluded mega-herbivores (O, C, W, WC). The mega-herbivore treatments (MW and MWC) were omitted because the KLEE experimental layout was not fully crossed. The results showed that there was no significant effect of cattle or meso-herbivores on relative vegetation cover and the resulting interaction was not significant (Fig. 3). How-

ever the mesoherbivores had a near significant negative effect on relative vegetation cover (Fig. 3).

**Spiders.**—Only the presence of cattle had a negative effect on spider abundance from sweep-netting samples ( $F_{1,500} = 5.84, P = 0.016$ ). The presence of mesoherbivores had no significant effect on abundance of spiders from sweep-netting samples ( $F_{1,500} = 5.84, P = 0.177$ ). Similarly, an ANOVA to test the effects of cattle and mega- and meso-herbivores on spider richness (total number of species) revealed that only the presence of cattle had a significant negative effect on sweep-netting samples ( $F_{1,332} = 6.05, P = 0.014$ ), (Fig. 4). Only the presence cattle had a significant negative effect on Shannon-Wiener diversity from sweep-netting samples ( $F_{1,332} = 4.68, P = 0.031$ ).

There was a positive, significant correlation between relative vegetation cover and Pielou’s evenness index and the Shannon-Wiener diversity index for sweep-netting samples (Table 2). Diversity indices from pitfall-trapping samples were not significantly related to relative vegetation cover (Table 2).

Four study species were chosen for individual analysis based on the fact that they were the most numerically dominant and represented a number of different functional groups: *Cyclosa insulana* (Costa 1834), *Argiope trifasciata* (Forskål 1775) (both Araneidae), *Runcinia flavida* (Simon 1881) (Thomisidae), and *Aelurillus* sp. (Salticidae). A series of analyses of covariance (ANCOVA) were performed to establish their response to some biotic and abiotic factors, namely relative vegetation cover, total monthly rainfall and presence of large mammalian herbivores. The

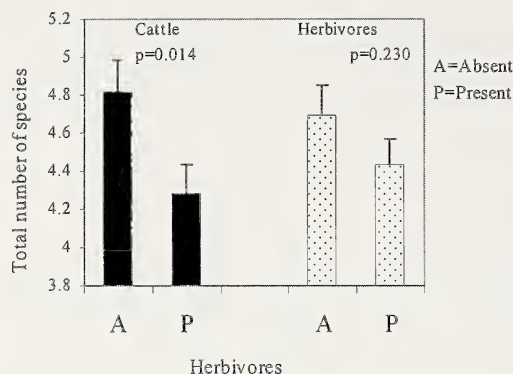


Figure 4.—Effects of ‘cattle’ (levels: absent [O, W and MW] vs. present [C, WC and MWC]) and ‘herbivores’ (levels: herbivores absent [O and C], only mesoherbivores present [W and CW], and both meso- and mega-herbivores present [MW and MWC]) on total number of spider species from sweep-netting samples (mean + SE). No treatments were omitted from the data set. The interaction term was not significant ( $P = 0.81$ ).

summarized results are shown in Table 3. The presence of cattle and meso-herbivores had significant, negative effects on the abundance of all of the species except *Aelurillus* sp., where the presence of cattle was related to an increase in the species’ abundance. Only *R. flavida* and *Aelurillus* sp. were significantly affected by the amount of rainfall (Table 3).

Finally, the stress values of multidimensional scaling (MDS) ordinations for the sweep-netting (Fig. 5) and pitfall-trapping data sets were 0.15 and 0.01, respectively, which implies that the plots were reliable two-dimensional representations of the n-dimensional similarities of the samples and therefore worth interpreting (Clarke & Warwick 1994). The aim of this analysis was to show whether the spider community organised itself in pattern that reflected the intensity of grazing by different herbivore groups. The MDS ordinations for sweep-netting samples have a clearer separation into three clusters of control, cattle and non-cattle grazing, (Fig. 5) when compared to pitfall-trapping samples (not shown) which did not separate by herbivore grazing group. For sweep-netting samples, only the southern control plot was peculiar (Fig. 5) and appeared to be in the same position as the cattle grazing plots. The other two control plots are in their own well-separated cluster. Grazing and control plots are separated by meso-

Table 2.—Correlations between relative vegetation cover and four measures of diversity (Shannon-Wiener diversity index [ $H'$ ], Margalef’s richness index [ $d$ ], Pielou’s evenness index [ $J'$ ] and total spider species [ $S$ ]) for data sets generated at Laikipia, Kenya in 2001–2002 using sweep-netting and pitfall-trapping samples.  $df = 18$ . \* = Significant at  $\alpha = 0.05$ .

Method	Diversity		
	index	r-value	P-value
Sweep-netting samples	S	0.35	0.160
	d	3.14	0.204
	$J'$	0.54	0.020*
	$H'$	0.61	0.007*
Pitfall-trapping samples	S	0.29	0.244
	d	0.26	0.304
	$J'$	0.06	0.809
	$H'$	0.23	0.356

herbivores (W) and mega-herbivore (M) treatment plots. For the pitfall-trapping data most cattle-grazing and non-cattle grazing plots overlapped, thus no interpretation could be made.

## DISCUSSION

There is considerable evidence that grazing and trampling have an influence, and in virtually all cases a negative one, on spider diversity (Gibson et al. 1982, 1992; Curtis et al. 1990; Abensperg-Traun et al. 1996; Rivers-Moore & Samways 1996; Abrous-Kherbouche et al. 1997; Fabricius 1997; Churchill 1998; Fabricius et al. 2002). Yet, this is the first paper that compares the influence of domesticated animals on spiders with that of wildlife. Our analyses (Table 1 and Figs. 2–4) support the conclusion that the presence of cattle, much more than that of other large mammalian herbivores, reduces relative vegetation cover and spider diversity and abundance, while other results (Table 2) demonstrate that diversity and species richness are correlated with relative vegetation cover. As expected, the presence of herbivores had an indirect effect on spiders, presumably by reducing the relative vegetation cover and hence the complexity of the habitat.

Spiders were significantly scarcer in the treatments with cattle compared to those with other large mammalian herbivores. However, some of the effects by mega- and meso-herbivores were close to significance suggesting



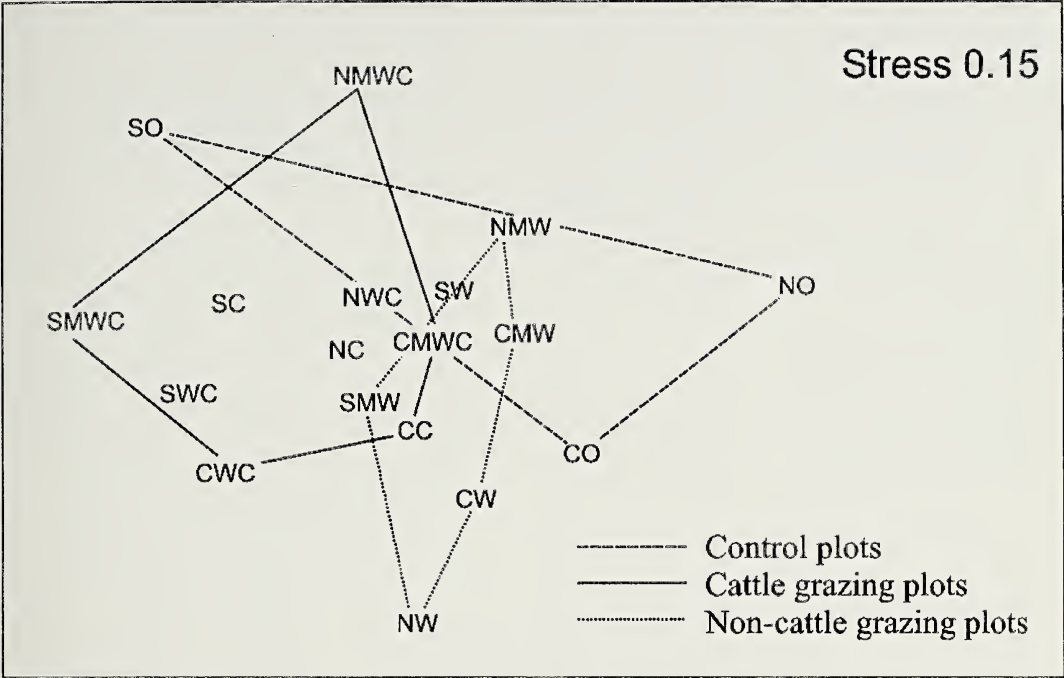


Figure 5.—Multidimensional scaling (MDS) ordination of the spider community in the sweep-netting samples of spiders collected at Laikipia, Kenya in 2001–2002, with convex hulls superimposed to enclose regions characteristic of control, cattle and non-cattle treatments. In all cases the first letter of any code represents the three study blocks, namely north (N), central (C) and south (S). All other letters represent the animals present, where O = control, C = cattle, W = meso-herbivores, and M = mega-herbivores.

that this group also had effects on spiders. Earlier research in the KLEE experiment has shown that exclosure of ungulates (control plots) resulted in a 60% increase in the total number of small mammals (Keesing 2000). In most cases, mega-herbivores (elephant, giraffe) influence the type of habitat under study by browsing its shrub and tree layer (Dublin 1995). Perhaps both mega-herbivores and meso-herbivores have little effect in the current study because they have low densities compared to cattle. It is already documented that most wildlife in Laikipia lives outside national parks (Western 1989; Mbugua 1986; LWF 1996). However, the densities of wildlife on ranches are considerably lower than that of livestock. This may be why only cattle densities were high enough to cause a statistically significant effect on the relative vegetation cover and, by extension, on the spider community.

The diversity indices from pitfall-trapping samples were not significantly related to relative vegetation cover unlike those from

sweep-netting samples. Such difference between the two methods may be caused by the difference in biology of the species targeted by the two methods. It was possible that sweep-netting mainly caught foliage dwelling spiders, which were likely to be affected by changes in vegetation cover more than ground living spiders that dominated the pitfall trap samples.

The influence of experimental treatments or abiotic environmental variables could be tested for only a few abundant species. *Cyclosa insulana* reacted to changes in relative vegetation cover, while *R. flavida* and *Aelurillus* sp. were more sensitive to seasonal changes. All four species including *A. trifasciata*, were significantly affected by the presence of cattle but in different ways. *Aelurillus* sp. was more abundant in plots grazed by cattle, while the reverse was true for the other three species. The specific behavior of each species (e.g., its way of acquiring food), or the kind of habitat where it lives may explain this difference. *Aelurillus* is a ground-active jumping spider that

Table 3.—Analysis of covariance (ANCOVA) to establish the effects of the factors ‘meso-herbivores’ (levels: absent [O and C] vs. present [W and WC]) and ‘cattle’ (levels: absent [O and W] vs. present [C and WC]) and two covariates, relative vegetation cover and total monthly rainfall, on the abundance of *Cyclosa insulana*, *Argiope trifasciata*, *Runcinia flavida* and *Aelurillus* sp recorded at Laikipia in 2001–2002. The codes for the above abbreviations are such that O = control (no large mammalian herbivores); (W) = meso-herbivores; (M) = mega-herbivores and (C) = cattle. \* = Significant at  $\alpha = 0.05$ .

Effect	Mean abundance $\pm$ SE		df	MS	F-value	P-value
	Absent	Present				
<i>Cyclosa insulana</i>						
Intercept			1	107.23	128.15	<0.01*
Relative vegetation cover			1	41.46	49.55	<0.01*
Total monthly rainfall			1	2.39	2.86	0.09
Cattle	1.73 $\pm$ 0.06	1.94 $\pm$ 0.05	1	3.52	4.21	0.04*
Meso-herbivores	1.82 $\pm$ 0.06	1.99 $\pm$ 0.05	1	0.42	0.51	0.48
Cattle*Meso-herbivores	1.89 $\pm$ 0.09	1.96 $\pm$ 0.07	1	2.82	3.36	0.07
Error			498	0.84		
<i>Argiope trifasciata</i>						
Intercept			1	5.09	32.64	<0.01*
Relative vegetation cover			1	0.00	0.01	0.92
Total monthly rainfall			1	0.54	3.46	0.06
Cattle	1.01 $\pm$ 0.02	0.88 $\pm$ 0.02	1	1.47	9.44	0.02*
Meso-herbivores	0.99 $\pm$ 0.03	0.92 $\pm$ 0.01	1	0.49	3.15	0.08
Cattle*Meso-herbivores	1.00 $\pm$ 0.03	1.04 $\pm$ 0.06	1	0.04	0.28	0.60
Error			498	0.16		
<i>Runcinia flavida</i>						
Intercept			1	6.06	25.29	<0.01*
Relative vegetation cover			1	0.58	2.43	0.12
Total monthly rainfall			1	3.75	15.64	<0.01*
Cattle	1.16 $\pm$ 0.03	1.00 $\pm$ 0.02	1	1.27	5.28	0.02*
Meso-herbivores	1.07 $\pm$ 0.03	1.08 $\pm$ 0.02	1	0.09	0.38	0.54
Cattle*Meso-herbivores	1.02 $\pm$ 0.04	1.11 $\pm$ 0.05	1	0.25	1.04	0.31
Error			498	0.23		
<i>Aelurillus</i> sp						
Intercept			1	8.54	37.44	<0.01*
Relative vegetation cover			1	0.02	0.09	0.77
Total monthly rainfall			1	0.89	3.89	0.04*
Cattle	1.05 $\pm$ 0.03	1.21 $\pm$ 0.03	1	2.84	12.46	<0.01*
Meso-herbivores	1.08 $\pm$ 0.03	1.15 $\pm$ 0.02	1	0.63	2.75	0.09
Cattle*Meso-herbivores	0.98 $\pm$ 0.04	1.18 $\pm$ 0.05	1	0.11	0.49	0.48
Error			498	0.23		

does not build webs to catch prey but chases and jumps onto prey. It seems likely then that it thrived well where there was more grazing and more open ground, compared to a web-builder like *Argiope* that preferred a complex habitat where it could find vegetation to anchor its web. Since *Aelurillus* is known to feed on ants, perhaps grazing makes ants more abundant and this in turn makes *Aelurillus* increase in abundance. Other related studies on individual species have shown that species

level of resolution has a limitation when used for such analysis since a single species tolerant of a perturbation might strongly influence the results (Caro and O'Doherty 1999). This was noted in the current study, where *C. insulana* was found to be very dominant.

The pattern shown by MDS analysis (Fig. 5) seems to correspond with the relative vegetation cover distribution pattern, which is found to be lower in grazing plots and higher in control plots. This could mean that the spi-



der community was responding to habitat complexity, including the factor “vegetation cover.” As already explained, control plots had the highest relative cover followed by meso- and mega-herbivore plots, while cattle plots had the lowest cover. The non-cattle grazing plots had intermediate vegetation cover, probably because wildlife were rarer than cattle in the experimental plots.

This general trend of the spider community to cluster along control, non-cattle grazing and cattle grazing zones in an MDS analysis (although true for only the herb layer fauna) agrees with earlier studies indicating that habitat complexity influences the distribution of spiders of the herb layer. For example, work by Halaj et al. (2000) reported that structural habitat complexity had a profound effect on canopy spiders and other arthropods. Rypstra (1983) and Wise (1993) concluded that spider populations are limited by the availability of unique structural features in the habitat rather than by the abundance of prey.

Exclosure treatments allowed us to detect changes in plant cover, and showed them to be significant in plots with cattle grazing. Plant cover appears to significantly affect spider diversity. Overall, activity by wildlife (mega- and meso-herbivores) had less (non-significant) effect on plant cover and spider diversity compared to that of cattle. The spider fauna of the black cotton soil savanna habitat is sufficiently rich to be useful for biological monitoring work in the sense of Kremen et al. (1994), who stated that: “the importance of monitoring is to come up with indicators that respond to anthropogenic disturbances early enough before changes manifest themselves in the more complex food webs and food chains and even affect the long living organisms.”

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## SPIDER (ARANEAE) COMMUNITIES OF SCREE SLOPES IN THE CZECH REPUBLIC

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**ABSTRACT.** We assessed the effects of environmental factors on spider communities in screes (sloping mass of coarse rock fragments) of the Czech Republic, based on catches from 325 pitfall traps, exposed for 177–670 days, from 1984–2000. Bootstrap resampling was applied to test for fuzziness of the partitions in cluster analysis of the samples. Two distinct spider communities were identified. The first one was confined to sites where ice is formed and persists until late summer or over the whole year. This community consists of numerous relict spiders, such as *Bathypantes simillimus buchari* Růžička 1988, *Diplocentria bidentata* (Emerton 1882) and *Lepthyphantes tripartitus* Miller & Svatoň 1978, possibly persisting in these cold screes from the early postglacial period. The other community included all other sites, irrespective of their environmental characteristics. Monte Carlo simulations were used to test the significance of environmental factors and their interactions on the studied communities. Ice formation near the traps and position of the traps within individual screes were the most significant factors, followed by the depth of the traps within the scree, diameter of stones forming the scree, and altitude. A marginally significant effect was found for organic content in the scree matter, whereas presence of trees and phytogeographical districts appeared non-significant. Our analyses support the view that spiders inhabiting cold screes in Central Europe belong to a unique relict community of species requiring cold and stable microclimate.

**Keywords:** Scree slopes, environmental factors, ice formation, CCA, Monte Carlo simulations

At middle elevations scree slopes (or talus, an accumulation of coarse rock debris that rests against the base of an inland cliff; Allaby & Allaby 2003) represent common terrain forms in larger parts of Europe. Most stone accumulations result from frost weathering of primarily compact rocks. These screes are widespread especially in the subarctic and in mountains in mid-latitudes, where a periglacial climate (i.e., climate of areas adjacent to a glacier or ice sheet) prevailing in the recent geological past promoted their development. Screes situated at middle elevations have attracted the attention of ecologists only recently, perhaps due to logistic constraints (difficult access, a permanent danger of falling stones, landslides, etc.). Relatively small cavities situated deeply in the scree are usually covered by unstable layers of stones, making non-destructive studies rather difficult or almost impossible. Further, the low densities of most invertebrates colonizing the inner parts of screes make short-term studies inefficient. In spite of these difficulties, current ecological research

showed that some of the screes host peculiar and surprisingly species-rich fauna of invertebrates. Recent ecological studies demonstrated that the screes represent island-like ecosystems, supporting species which do not occur in the surrounding areas (Möseler & Molenda 1999; Kubát 2000). Repeated field observations supported by microclimatic measurements have shown that some screes function as large coolers, accumulating cold air that persists in some parts of the screes over the whole season. The thermic regime of the screes is often extremely conservative, largely independent of temperature fluctuations above-ground, both within and between years. At the bottom of some screes ice is formed, sometimes persisting there over the whole year, even if temperatures above-ground are higher by 30 °C or even more (Gude et al. 2003). Therefore, the stability of the temperature regime with extremely cold temperatures throughout the year and permanently high humidity enables persistence of a unique community of invertebrates, including



several representatives of arctic fauna which retreated from other habitats in Central Europe more than 10,000 years ago.

The research focused on the fauna of invertebrates in screes of the Czech Republic was considerably intensified after modified pitfall traps were developed (Růžička 1982, 1988b). These traps were exposed by the senior author for several months up to two years in most important scree localities in the country over the course of the last two decades. Numerous surprising findings have been reported, based on this research, including twelve species of spiders, mites and diplopods new to the Czech Republic (Růžička 1988b, 1994, 2000, 2002; Růžička et al. 1989; Růžička & Antuš 1998; Růžička & Hajer 1996; Zacharda 1993) and five species/subspecies new to science (Růžička 1988a; Zacharda 2000a, b, c). The results of the studies carried out on nearly 66 localities revealed also a considerable heterogeneity of spider communities inhabiting the screes. While some localities host numerous relict species (see Discussion), other sites are relatively poor in biogeographically and ecologically interesting spiders. Also, a considerable variation was observed within individual localities, with great differences between individual parts of the screes. These observations resulted in several ecological questions that we address in this paper: 1) What are the environmental factors responsible for the observed variation in species composition of spider assemblages in the screes? 2) Is the occurrence of relict species in screes correlated with some environmental factors? 3) Is there a sharp boundary between spider communities of cold and warm sites within individual screes?

To answer these questions we compiled all available records of spiders from screes of the Czech Republic, obtained by pitfall traps exposed for a longer time, and added available information on environmental factors, either measured or estimated in other ways at sites where the spiders were collected. This resulted in a relatively large and complete dataset which we used in the analysis.

## METHODS

**Study area and localities.**—The Czech Republic is situated in the temperate zone of Europe between 48° 33' and 51° 03' N, and 12° 05' and 18° 51' E. Major parts of the

Czech Republic belong to the Proterozoic and Palaeozoic Bohemian Massif, only the easternmost part is pervaded by the Tertiary mountain system of the western Carpathians. The Bohemian Massif was long ago transformed by erosion into a levelled terrain, which was, during the Alpine formation of mountains, disrupted by faults, fractures in rock strata; elevated crustal blocks formed mountain regions (particularly border mountains), and the volcanic region of České Středohoří Mts. in the north of the Czech Republic was formed. The system of deeply cut river valleys was formed during the Tertiary and, especially, during the Quaternary (Ložek 1988). Due to its geology and geomorphology, the territory of the Czech Republic is rich in various boulder accumulations (Růžička 1993).

Material was collected from 66 localities distributed all over the Czech Republic (Fig. 1). Elevations of the localities ranged from 270–1550 m a.s.l. The investigated screes are formed by andesite, basalt, conglomerate, limestone, phonolite, quartzite, sandstone, granite and other kinds of rock. The height of scree fields from the foot to the top varied between 10 and 250 m, slope angles ranged between 20° and 40°.

**Sampling.**—The animals were usually trapped in modified pitfall traps made of rigid plastic (Růžička 1982, 1988b). The traps consisted of a board (20 x 25 cm), which forms an artificial horizontal surface (note that a flat horizontal soil surface is not present in scree slopes) and a can inserted in the centre of the board. Traditional pitfall traps (simple cans) were also used. The cans contained a mixture of 7% formaldehyde and 10% glycerol with a few drops of a surfactant. The traps were placed among the stones. Field research was conducted from 1984–2000. In total, 325 traps were installed, most of them (85%) for more than 300 days.

The catch, especially from deeper scree layers, is often poor in species. To obtain more representative samples, we combined catches from traps placed at the same position along the scree slope in individual localities. This resulted in 128 samples.

**Environmental characteristics.**—In total, eight environmental characteristics were registered: elevation (m a.s.l.); scree type (1 = bare scree slopes, 2 = scree slopes partly

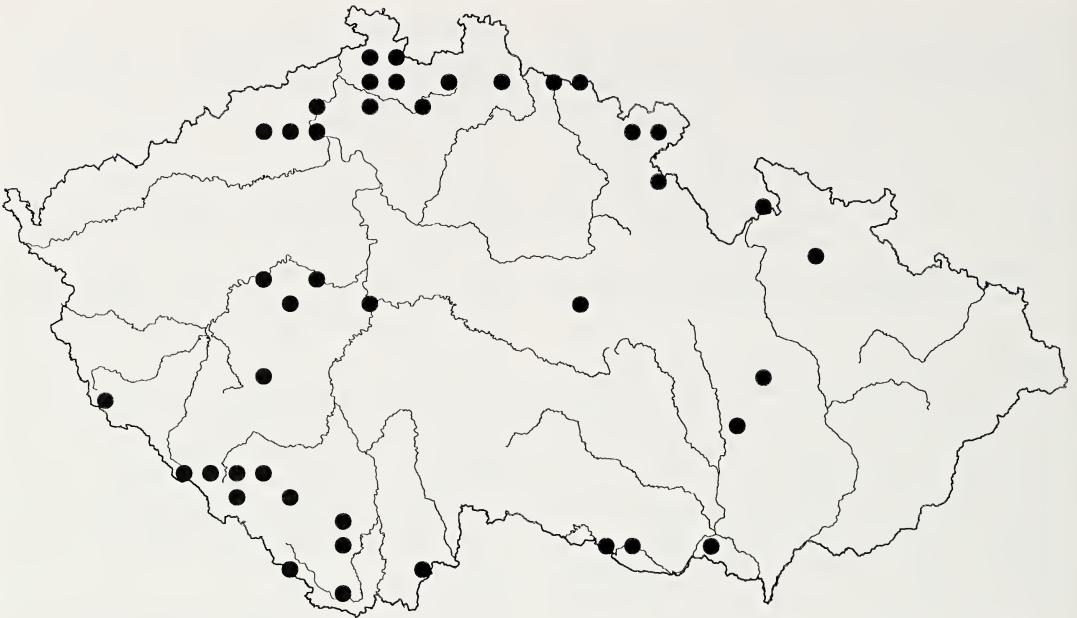


Figure 1.—Location of the studied screes on a grid map of the Czech Republic. The circles represent one or several localities used in the analysis.

overgrown by solitary trees, 3 = scree forests, corresponding to a gradient from bare to forest screes); position of pitfall traps along the temperature gradient in scree field (1 = lower margin, 2 = middle part, and 3 = upper margin of the scree); ice formation near the trap (1 = no ice formation, 2 = temporal ice inside scree, melting in summer, 3 = permanent ice forming permafrost-like conditions); typical size of stones in the scree (diameter ranging from 0.1–10 m); depth below the surface in which the trap was installed (ranged from 0–5.0 m); substrate around the trap (1 = bare stones, 2 = soil, 3 = detritus, 4 = mosses, ranges from sterile to organic substrate); phytogeographical district (1 = thermo-, 2 = meso-, 3 = oreophyticum, characterized by vegetation on a broader scale, Slavík 1984).

In addition, three covariables were used: type of trap (1 = a pot, which was a low efficiency trap; 2 = a pot sunken into a board, which was considered a high efficiency trap); number of traps at a site (ranging from 1–11); number of days during which the trap was exposed.

**Data analysis.**—In the numerical analyses we always used the whole data set, i.e., all localities and all species. The input data were log-transformed prior to analysis. Detrended

Canonical Correspondence Analysis (DCA) was used to estimate species turnover along the main direction of variability. After that CCA (Canonical Correspondence Analysis) implemented into the CANOCO program (ter Braak & Šmilauer 1998) was performed to test the effects of individual variables and their interactions on species composition. Monte Carlo simulations with 10,000 permutations were calculated to assess the significance of individual environmental factors and their interactions. In these analyses the factors which were not used as explanatory variables were defined as covariables, to remove their effects on the results and to obtain a net effect of individual environmental variables. Using this approach we could perform tests that are counterparts to ANOVA but for multivariate data.

Spider communities were classified by a cluster analysis based on Ward's method, using Euclidean distances for quantitative data (Jongman et al. 1995, p. 178), calculated for log-transformed catches, using the Syn-tax program by Podani (2001). The sharpness of the resulting classification was tested using a bootstrap resampling, in which stability of partition at a given level was tested by resampling the original data, according to Pillar



(1999). The outcome of this testing indicates whether groups in the partition reappear more often in resampling data than expected on a random basis.

Nomenclature follows the catalogue of spiders of the Czech Republic (Buchar & Růžicka 2002). Species characteristics were also taken from this source. Voucher specimens are deposited in the collection of V. Růžicka.

## RESULTS

**Site characteristics.**—The strongest significant correlation between pairs of the eight environmental characteristics was found between elevation and phytogeographical district ( $r = 0.70$ ). This reflects the crucial role of elevation in the distribution of plant communities at a broader scale. The position of the traps was strongly negatively correlated with the incidence of ice at the traps ( $r = -0.49$ ), implying that traps situated at the lower margin of the screes were often surrounded by permanent ice whereas traps placed at the upper margin were free of ice. As expected, bare scree slopes were usually built of large boulders whereas forested screes developed on gravel screes ( $r = 0.40$ ). Further, scree sites with large amounts of organic matter and covered by mosses usually developed in warm regions ( $r = -0.32$ ), at lower elevations ( $r = -0.34$ ) and at the lower margin of the screes ( $r = -0.35$ ).

Ice formation was negatively correlated with elevation ( $r = -0.20$ ). Even if elevations of the sites (270–1550 m) spanned the range of elevations in the Czech Republic almost completely, surprisingly the screes with ice formation were found at rather low elevations; the screes with permanent ice filling were situated at 350–650 m a.s.l., the screes with temporal ice filling at 270–700 m a.s.l. The ice was found more often in sterile screes without organic matter and deeper in the scree than in screes with organic matter and near traps situated closely to the scree surface ( $r = 0.26$  and  $r = -0.21$ , respectively). All these correlations were significant at  $P < 0.05$ .

**Species composition.**—In total, 1047 spiders were captured, belonging to 176 species of 22 families. Based on our knowledge on ecological demands of all spider species in the Czech Republic (Buchar & Růžicka 2002), the following sets of species can be identified among the captured spiders:

1. Species occurring exclusively in bare scree slopes (and in adjacent underground spaces) and in scree forests: *Acantholycosa norvegica* (Thorell 1872), *Bathyphantes similis buchar* Růžicka 1988, *Clubiona alpica* Kulczyński 1882, *Comaroma simoni* Bertkau 1889, *Diplocentria bidentata* (Emerton 1882), *Kratochviliella bicapitata* Miller 1938, *Lepthyphantes notabilis* Kulczyński 1887, *Lepthyphantes improbulus* Simon 1929, *Lepthyphantes zimmermanni* Bertkau 1890, *Liocranum rutilans* (Thorell 1875), *Meta menardi* (Latreille 1804), *Micrargus apertus* (O. P.-Cambridge 1871), *Neon levis* (Simon 1871), *Pholcomma gibbum* (Westring 1851), *Porrhomma myops* Simon 1884, *Porrhomma rosenhaueri* (L. Koch 1872), *Rugathodes bellicosus* (Simon 1873), *Saaristoa firma* (O. P.-Cambridge 1905), *Trogloneta granulum* Simon 1922, *Wubanoidea uralensis* (Pakhorukov 1981).

2. Species of scree slopes, occurring also in other habitats (in brackets): *Lepthyphantes leprosus* (Ohlert 1865), *Liocranum rupicola* (Walckenaer 1830), *Nesticus cellulanus* (Clerck 1757), *Pholcus opilionoides* (Schränk 1781), *Sitticus pubescens* (Fabricius 1775) (synanthropic), *Ceratinella major* Kulczyński 1894, *Megalepthyphantes collinus* (L. Koch 1872), *Tegenaria silvestris* L. Koch 1872 (forests), *Lepthyphantes tripartitus* Miller & Svatoň 1978, *Theonoe minutissima* (O. P.-Cambridge 1879) (peat bogs), *Agraeocina striata* (Kulczyński 1882) (lowland forests), *Walckenaeria capito* (Westring 1861) (rock steppes), *Cryphoea silvicola* (C.L. Koch 1834) (spruce forests), *Porrhomma egeria* Simon 1884 (caves and subalpine belt).

The cluster analysis of samples revealed two distinct groups, indicating that two clearly separated spider communities can be identified in the screes (Fig. 2). The bootstrap resampling showed a partitioning at this level. For lower levels, i.e. when considering partitioning to a higher number of clusters, we obtained non-significant results. Accordingly, all clusters except for those labelled in Fig. 2 A and B should be interpreted as fuzzy, not distinctly separated from each other. All ten samples from sites at which permanent ice was observed and most samples from sites at which temporal ice formation was registered were included in cluster A. The other cluster, B, included all other localities.





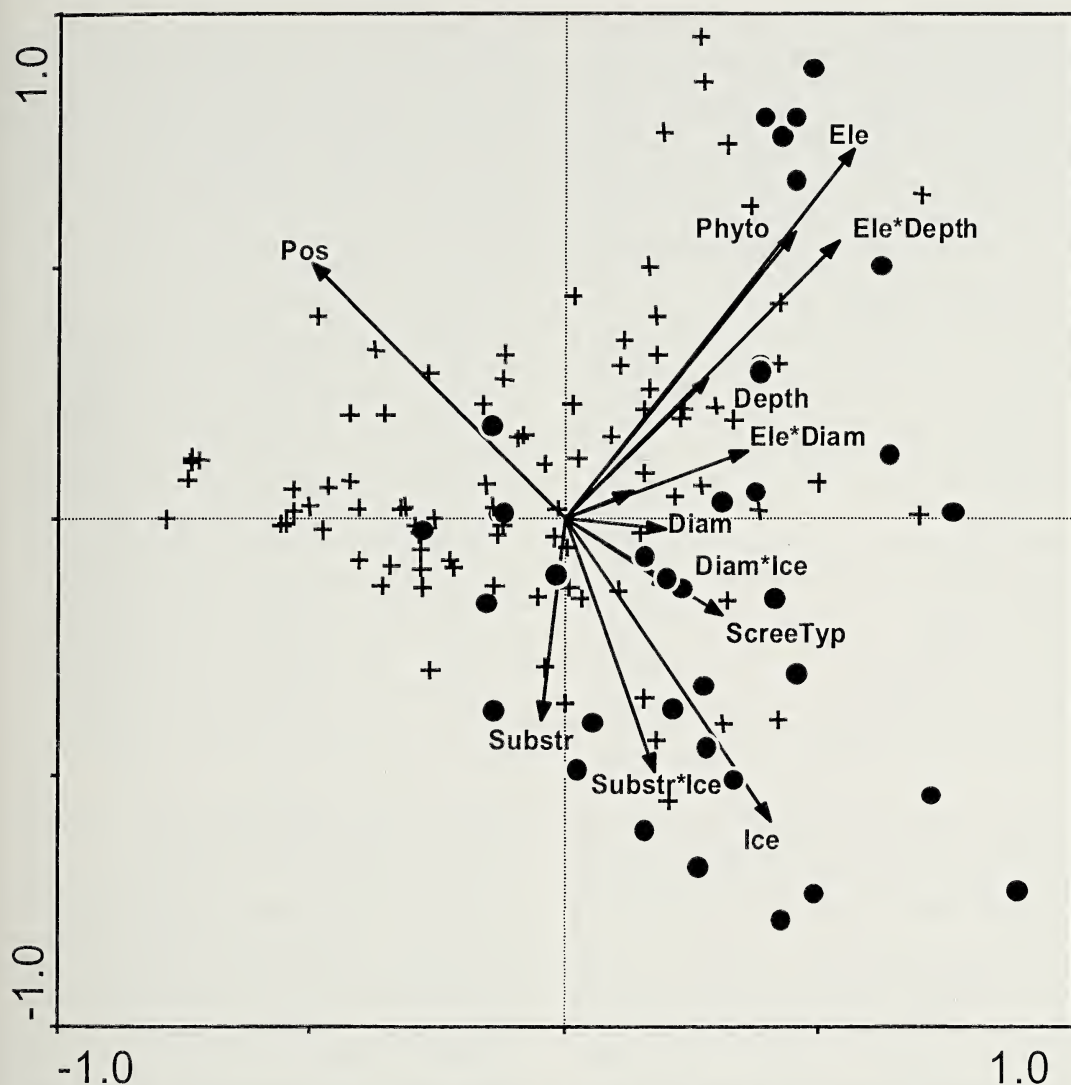


Figure 3.—CCA ordination of samples. Arrows indicate the effect of environmental variables. Full circles = samples belonging to A cluster in Fig. 2, crosses = samples belonging to B cluster. ELE: elevation; ICE: ice formation near the trap; DEPTH: depth below the surface, in which the trap was installed; POS: position of pitfall trap along the temperature gradient in scree field; DIAM: typical size of stones; SUBSTR: substrate around the trap; PHYTO: phytogeographical district; SCREETYP: from bare scree to scree forest.

relatively high number of samples scattered over the whole Czech Republic enabled a more detailed analysis of the effect of environmental factors on individual species.

Analyses of the relationship between environmental variables and the number of captured spiders of individual species (linear regression) showed that species found mainly at higher elevations included *Clubiona alpicola* (only above 700 m a.s.l.), *Wubanoides uralensis* (only above 930 m), *Bathyphantes sim-*

*illimus*, and *Walckenaeria capito*. Several species were caught mainly at lower elevations: *Lepthyphantes improbulus* (up to 400 m a.s.l.), *Pholcus opilionoides* (up to 750 m), *Liocranum rupicola* (up to 800 m) and *Pholcomma gibbum*.

*Metellina merianae* occurred primarily in scree forests; *Acantholycosa norvegica*, *Lepthyphantes notabilis*, *Clubiona alpicola* were recorded exclusively on bare, open scree slopes.

Table 1.—Results of the CCA analyses applied to log abundances of spiders caught in pitfall traps. *r*: species-environment correlation on the first axis, *var*: percentage of species variability explained by the first ordination axis, *F*: the *F*-ratio statistics for the test on the trace, *P*: corresponding probability value obtained by the Monte Carlo permutation test. The variables not used as explanatory variables in individual analyses, were used as covariables. Type of the trap, number of traps at a site and number of days for which the trap was exposed were used as covariables in all analyses. *ELE*: elevation; *ICE*: ice formation near the trap; *DEPTH*: depth below the surface, in which the trap was installed; *POSITION*: position of pitfall trap along the temperature gradient in scree field; *DIAM*: typical size of stones; *SUBSTR*: substrate around the trap; *PHYTO*: phytogeographical district; *SCREETYP*: from bare scree to scree forest.

Explanatory variables	<i>r</i>	<i>var</i>	<i>F</i>	<i>P</i>
<i>ELE</i>	0.812	1.5	1.67	0.0017
<i>ICE</i>	0.828	1.7	1.84	0.0001
<i>DEPTH</i>	0.833	1.4	1.54	0.0003
<i>POSITION</i>	0.803	1.7	1.87	0.0001
<i>DIAM</i>	0.809	1.4	1.59	0.0089
<i>SUBSTR</i>	0.8	1.2	1.3	0.0497
<i>PHYTO</i>	0.732	0.9	1.03	0.3920
<i>SCREETYP</i>	0.767	0.9	0.95	0.5951
<i>ELE</i> × <i>DIAM</i>	0.778	1.3	1.47	0.0215
<i>DIAM</i> × <i>ICE</i>	0.843	1.4	1.54	0.0185
<i>SUBSTR</i> × <i>ICE</i>	0.847	1.3	1.42	0.0192
<i>ELE</i> × <i>DEPTH</i>	0.809	1.3	1.38	0.0323
<i>SUBSTR</i> × <i>DEPTH</i>	0.81	1.2	1.3	0.0396
<i>PHYTO</i> × <i>SUBSTR</i>	0.774	1.1	1.23	0.1060
<i>SCREETYPE</i> × <i>SUBSTR</i>	0.783	1	1.07	0.3015

*Lepthyphantes notabilis* and *Pholcus opilionoides* colonized mainly upper scree margins; *Lepthyphantes tripartitus* and *Diplocentria bidentata* occurred mainly at lower margins.

The dependence on ice formation is sharp in some spiders: *Rugathodes bellicosus*, *Lepthyphantes notabilis*, *Tegenaria silvestris*, *Nesticus cellulanus*, *Pholcomma gibbum*, *Meta menardi*, *Acantholycosa norvegica*, *Lio-cranum rupicola*, *Pholcus opilionoides* avoided sites with ice formation, whereas *Lepthyphantes tripartitus*, *Diplocentria bidentata* and *Bathypantes similimus buchari* at lower elevations were confined to these sites.

*Diplocentria bidentata* and *Lepthyphantes tripartitus* occurred together at sites where ice is formed. Along the gradient of substrate type, *L. tripartitus* preferred more detritus-rich sites, whereas *D. bidentata* colonised more mossy habitats. *Diplocentria bidentata* tended to occur at the surface, whereas *L. tripartitus* occurred in deeper layers. These trends were univocally supported by the separate sieving of moss and detritus on Klíč Mt. on 12th October 1999: 28 specimens of *L. tripartitus* and 6 specimens of *D. bidentata* were collected by detritus sieving, whereas 66 specimens of *D.*

*bidentata* and 1 specimen of *L. tripartitus* were collected by moss sieving.

Orb weavers *Metellina merianae* and *Meta menardi* preferred spaces among larger stones; in contrast, *Lepthyphantes notabilis*, *Pholcomma gibbum*, *Acantholycosa norvegica* were more abundant at sites with smaller stones.

The species occurring mainly at the scree surface included *Acantholycosa norvegica*, *Diplocentria bidentata*, whereas *Porrhomma myops*, *Rugathodes bellicosus*, *Meta menardi*, *Nesticus cellulanus*, *Wubanoidea uralensis* were found mainly in the depth of the screes.

Finally, species found mainly at the surface of bare stones included *Lepthyphantes notabilis*, *Clubiona alpicola*, *Rugathodes bellicosus*, *Meta menardi*, *Theonoe minutissima*, and *Wubanoidea uralensis*.

## DISCUSSION

Balch (1900) was possibly the first who documented ice formation in scree slopes at middle (but not at higher) elevations. We showed that ice is regularly formed in screes also from 270–700 m. According to Gude et al. (2003) lower parts of scree slopes are intensively cooled during short periods of winter frost. Cold air penetrates inside the screes



only during periods with no (or limited) snow cover. Long-term data from three south Bohemian meteorological stations support this hypothesis. They indicate a negative relationship between the number of frost days without snow cover and altitude: there are 23 frost days without snow per year in České Budějovice at 389 m, 19 such days at Kašperské Hory (737 m) and only 10 frost days without snow per year on Churáňov at 1,118 m a.s.l. Mountain scree slopes do not markedly cool in winter, because frost air cannot penetrate the scree slopes through the snow cover.

Spatial heterogeneity of invertebrates in scree slopes was studied by Molenda 1989; Růžička et al. 1995; V. Růžička 1990, 1996, 2002; J. Růžička 1996. The position of a site along the scree slope was designated as the main factor influencing species distribution by Brabec (1973) in his pioneer study. We found that the effects of position of the trap on the scree slope and ice formation are strongly significant. Ice formation is a principal factor and ice is usually formed on the lower margin of scree slopes. However, concave slope forms can be formed by various slope denudation processes also in the middle part of a scree slope (Demek et al. 1975; Růžička 1999c). In such cases, ice can be formed also in the middle part of a scree slope.

Elevation patterns in spiders and mites of screes also have been documented by Růžička & Zacharda (1994) who focused on scree habitats in our highest mountains in the Krkonoše National Park, and by V. Růžička (1996), who studied spiders in screes at low elevations of the Podyjí National Park.

Spatial distribution of spiders in screes was studied by Růžička 1999a, 2002 and Růžička et al. 1995. Temperature is a key factor responsible for the presence or absence of species in individual parts along the slope. The dependence of *L. tripartitus* on detritus explains the fact, that this species colonizes the whole profile of the lower margin of the screes, from the surface to the depth of about one meter, whereas *D. bidentata*, which is restricted to moss cushions, cannot colonize deeper layers.

Land surfaces at higher latitudes in the northern hemisphere support a range of forest, scrub, tundra and peatland communities at the present day that may collectively be called the "coldland complex". Physiognomically and

floristically similar communities also occur at higher elevations of mountains further south (Tallis 1991). Current disjunct distribution of some spider species is a result of their withdrawal from Central Europe caused by changing climatic conditions in the Pleistocene. Twenty-seven spider species of the Czech arachnofauna exhibit boreo-montane type of geographical distribution (Růžička in prep.). They occur in higher latitudes and have disjunct, island-like populations in Central Europe. The present findings indicate that some scree spiders in Central Europe could be regarded as relicts of former climatic periods ("glacial relicts"). Four of these species occur exclusively in scree slopes (Buchar & Růžička 2002).

Having a distribution center in Siberia/North Asia, *Wubanoidea uralensis* and *Acantholycosa norvegica* occur only in several localities in Central Europe (Schikora 2004; Marusik et al. 2003), independent of ice formation. *Bathypantes similimus* shows about the same general distributional pattern. In contrast, *Diplocentria bidentata* has a Holarctic distribution. In Scotland, northern England and Wales it occurs locally with a low abundance in highlands (Harvey et al. 2002). In Central Europe it is known only from the peat bogs in Harz, Germany, situated at the highest elevations (Wiehle 1965); in the Czech Republic on hilltops in the Krkonoše Mountains (2 specimens) and on lower margin of frozen scree slopes (243 specimens). The occurrence of the latter two species is closely tied to ice formation in scree slopes. The same is true for the Central European mountain species *Lepthyphantes tripartitus*. The occurrence of the three species at lower elevations is closely tied to the present periglacial temperature regime in frozen scree slopes, and the presence of these species indicates the palaeorefugial character of these habitats (Zacharda et al. in press), i.e. island-like habitats inhabited by populations of formerly more widespread species (Nekola 1999).

Deep layers of screes represent shallow subterranean spaces, in which gradual adaptation to the stable environment of deep subterranean spaces takes place (Růžička 1999b). Species, which preferentially colonise deep scree layers, exhibit leg elongation, depigmentation, body diminishing, and eye reduction (Růžička 1988a, 1990, 1998; Schikora 2004).

We found some of these species on several localities (*R. bellicosus*, *B. s. buchari*); on the other hand, the occurrence of *Porrhomma myops* and *Comaroma simoni* is known from one locality only. The reason for their rarity (a special combination of environmental factors vs. our inability to penetrate more deep in scree?) remains unknown.

### ACKNOWLEDGMENTS

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## FAUNISTIC SIMILARITY AND HISTORIC BIOGEOGRAPHY OF THE HARVESTMEN OF SOUTHERN AND SOUTHEASTERN ATLANTIC RAIN FOREST OF BRAZIL

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**ABSTRACT.** Harvestmen show a high degree of endemism in the Atlantic Rain Forest (eastern coast of Brazil). This biome shows the highest diversity of harvestmen inhabiting Brazil; 2/3 of the species are found in this area. Most of the species are distributed in a few thousand square kilometers, almost always within one mountain range. The similarities of 26 localities were studied, including sites from the Brazilian savanna, using data from recent collections (more than 8,000 specimens) and published data. A cluster analysis using Sørensen's Coefficient indicated a high degree of endemism of species of harvestmen (similarity indexes below 0.5). It resulted in six main clusters related to the large mountain ranges and near sites. A high variation in richness was observed; 4–64 species per locality. The distribution of 84 species of four recently reviewed subfamilies of Gonyleptidae (Goniosomatinae, Caelopyginae, Progonyleptoidellinae and Sodreaninae) was studied. Eleven areas of endemism, with 3–14 endemic species each, were proposed. A primary Brooks Parsimony Analysis showed a possible first vicariant event splitting the fauna of two northern areas from the rest, and a second event splitting the fauna of southern areas (until 24°35'S) from those areas related to certain mountain ranges in the central Atlantic Rain Forest. The vicariant events were related to the uplifting of the Serra do Mar and the Serra da Mantiqueira, and the appearance of large rivers and climatic changes.

**Keywords:** Atlantic Rain Forest, biodiversity, Brooks Parsimony Analysis, harvestmen, Neotropics.

The Atlantic Rain Forest is located in the largest part of the Brazilian coastal region between 6–30° S, also occupying the central to southern interior part of the country. This biome comprises two types of vegetation formation: the Coastal Atlantic Rain Forest, close to the coast line, with elevations from sea level to approximately 1,000 m a. s. l., and with a hot, warm climate lacking a dry season; and the Atlantic Semi-deciduous Forest, which extends across the plateau in the interior of the country (usually above 600 m elevation), that can have a severe dry season, normally between April and September (Oliveira-Filho & Fontes 2000). The Atlantic Rain Forest was almost completely continuous in 1500, the year of the discovery of Brazil by Europeans, but is currently totally fragmented and reduced to less than 7.6% of the original area (Morellato & Haddad 2000). This occurred because colonization was mainly on the coast and most state capitals are in this biome. We

should stress that anthropogenic pressure is still strong on the remaining fragments. The few areas without or with a low anthropogenic pressure are in governmental reserves or in steep regions.

Diversity in the Atlantic Rain Forest seems to be higher than in most parts of the Amazonian Rain Forest, and endemism is remarkable; 50% on an average and as high as 95% in some groups of amphibians according to Morellato & Haddad (2000). However, such statements are mainly based on data for plants and vertebrates, the invertebrates remaining poorly studied. An examination of the records of Laniatores harvestmen of the Atlantic Rain Forest (see the catalog of Kury 2003) and Eupnoi (Tourinho-Davis & Kury 2003; Tourinho-Davis 2004) revealed that the group represents an exclusive fauna, with the highest level of endemism (97.5%) in this biome.

The opilionids are hygrophilous, have low vagility and are primarily nocturnal and cryp-



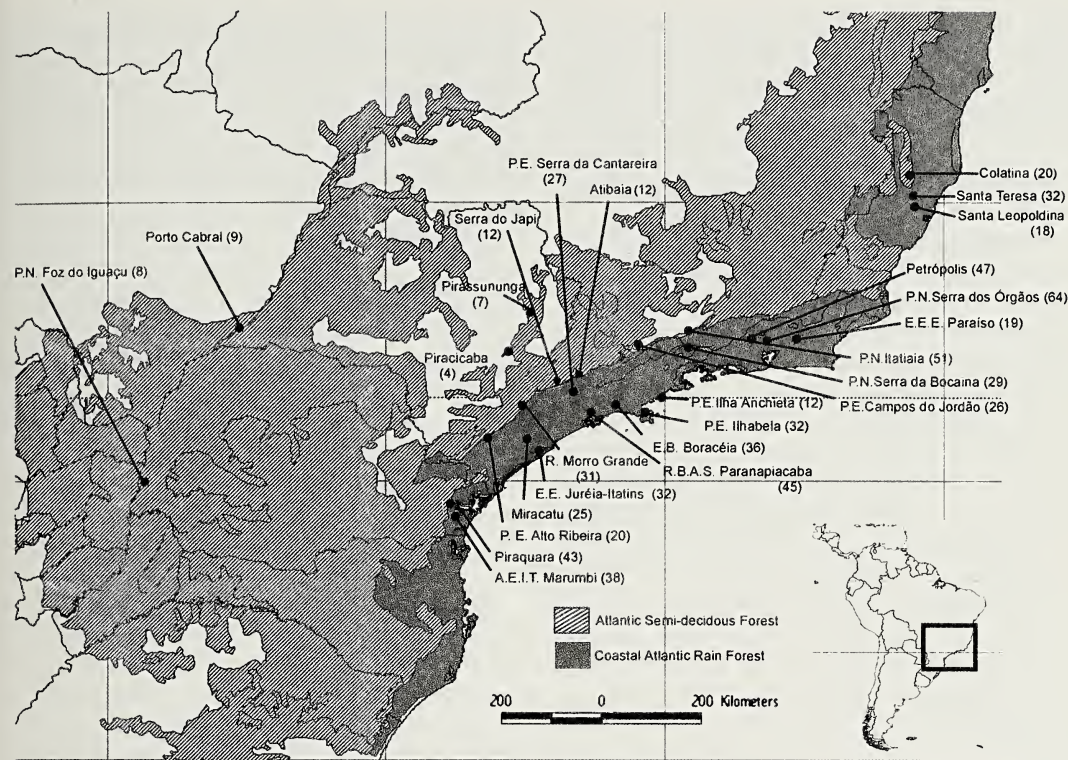


Figure 1.—Richness (between brackets) of Opiliones (Laniatores and Eupnoi) recorded in 26 localities in south and southern Brazil.

tic. Apparently the Laniatores possess low capability of dispersion. These aspects suggest the group is a good model for biogeographic studies. The only two studies dealing with opilionids which analyzed biogeography based on cladistic analysis were Briggs & Ubick (1989) and Ubick & Briggs (1989) for two genera of Laniatores, Phalangodidae, endemic to coastal California.

Few studies deal with historic biogeographic aspects of the Atlantic Rain Forest. Some studies related this biome as sister area with the Andean-Amazonian region (Amorim & Pires 1996) or as sister area with southern region (from São Paulo to Rio Grande do Sul) in case of groups with more southern occurrence in South America (Morrone et al. 1994; Pérez-Losada et al. 2004). A few biogeographic hypotheses based on phylogenetic reconstructions were proposed for the Atlantic Rain Forest, as the comprehensive studies of Costa (1995) for fishes and Amorim & Pires (1996) for dipterans and monkeys. The main goals of this article are to demonstrate the great diversity of opilionids in the Atlantic Rain Forest

including their high endemism, and to present a biogeographic hypothesis for the region.

METHODS

**Similarity and richness.**—The Sørensen index was applied to the analysis of similarity among the records of occurrence of 363 named species of Opiliones (Laniatores and Eupnoi) in 26 sites in south and southeastern Brazil. Morphospecies were not included because they were not standardized among all sites. The most intensively sampled sites were chosen, using the following criteria: more than 200 specimens collected; or stability or little increasing of richness with recent collecting. The analyses were performed with the MVSP 3.1 software (Kovach Computing Services 1999). The records were obtained from the literature (Laniatores from Kury 2003; Eupnoi from original descriptions and Tourinho-Davis 2004) in addition to museum records of the Museu de Zoologia da Universidade de São Paulo (MZSP), Instituto Butantan (IBSP) and Museu Nacional do Rio de Janeiro. These collections include old material and 8,879 spec-



imens recently collected (2000–2004) for the project Biodiversity of Arachnida and Myriapoda of the State of São Paulo (IBSP, MZSP). The observed richness of each locality (Fig. 1) was calculated including morphospecies, records from literature and material from museums.

**Biogeographic analyses.**—Four subfamilies of Gonyleptidae, for which we have cladistic hypotheses at species level (Goniosomatinae, Caelopyginae, Progonyleptoidellinae and Sodreaninae), were used for biogeographic analyses. The areas of endemism were chosen by overlapping areas of distribution of at least three endemic species. The areas of endemism basically follow Pinto-da-Rocha (2002) with some modifications: the component Santa Catarina (SC) was split from Paraná (PR); the southern region of São Paulo (SSP), located in the Vale do Ribeira was split from the Serra do Mar of São Paulo; and the Serra dos Órgãos (Org) was split from the Serra do Espinhaço (SEsp). Other abbreviations are: Bahia (BA), Espírito Santo (ES), lowlands of the northern part of the São Paulo coast and the southern part of Rio de Janeiro state (LSRJ), Serra da Bocaina (Boc), Serra da Mantiqueira (Mnt), Serra do Espinhaço (SEsp), Serra do Mar de São Paulo (SMSP), and Serra dos Órgãos (Org).

The primary Brooks Parsimony Analysis (BPA) was performed to infer relationships among areas. In this analysis each terminal of the species' cladograms was replaced by the species' areas of distribution; terminals and nodes were transformed into a binary matrix (Brooks et al. 2001). The function of primary BPA is to determine whether there is a general pattern among areas (Brooks et al. 2001). Widespread taxa were considered informative and their area considered as monophyletic (Assumption 0). The matrix of the area was constructed with the patterns of distribution of 84 species (Table 1) of two species cladograms: one for the subfamily Goniosomatinae; and another for the monophyletic group composed of the subfamilies (Sodreaninae (Progonyleptoidellinae, Caelopyginae)). The hypotheses of relationship among subfamilies of Gonyleptidae and species of Caelopyginae are in Pinto-da-Rocha (2002). The revisions and hypotheses for the Goniosomatinae (M.B. da Silva and P. Gnaspini), Sodreaninae and Progonyleptoidellinae (both R. Pinto-da-Ro-

cha) are in preparation for publication. Taxa cladograms (for species names see Table 1): Caelopyginae = (((7, 6)(2(4(3, 1)))) ((19(11(10(12(13(18)) (14(15, 16, 17)))))) (5(23(21(20, 22))) ((8, 9) (27(24, 25, 26)))))))); Goniosomatinae = (((((62, 63) ((50, 54) (64, 68))) ((67(51, 55)) (73(66(52, 65)))))) ((70(53(59, 75))) (60(57(49(56(61, 58)))))) (82(84((79(80(74, 78))) (77(83((71, 72) (81(69, 76)))))))); Progonyleptoidellinae = ((45, 46) ((48(47(41(40, 42)))) (36(43, 44)(35(37(38(34, 39)))))); Sodreaninae = (30(28(29(33(32, 31))))). The parsimony analysis of the biogeographic matrix was conducted with the PAUP 4.0 (Swofford 2002), using Branch-and-Bound algorithm with the commands hold10000, mult\*1000 and hold/1000.

## RESULTS

**Richness.**—Richness varied from 4–64 species per locality in south and southeastern Brazil (Fig. 1). The areas of low diversity are in cerrado forests (Brazilian savanna) with 4–7 species (Piracicaba and Pirassununga) and in the Atlantic Semi-deciduous Forest with 8–12 species (Foz do Iguaçu, Porto Cabral, Japi and Atibaia). Localities in the Coastal Atlantic Rain Forest are richer with 12–64 species. However, it must be stressed that some areas on the coast, such as Ilha Anchieta and Paraiso, were undersampled (40–50 h of nocturnal sampling) and there are no records either from literature or from museums. Thus, these estimates should be taken with care. Localities considered as well-sampled such as Cantareira, Morro Grande, Boracéia, Paranaipiacaba, Itatiaia and Serra dos Órgãos, present 27–64 species. Therefore, the fauna of harvestmen of the Coastal Atlantic Rain Forest is richer than the Atlantic Semi-deciduous Forest and the cerrado.

**Faunistic similarity.**—Analyses showed clusters among localities of the same mountain range (Fig. 2). From the 363 species included in the matrix, 213 (58.7%) occurred in just one locality. Among the 150 species recorded in more than one locality, only 93 were in two. Therefore, the groups possess only a few species in common, generating very low indices of similarities, thus indicating the high level of endemism of harvestmen species.

The fauna of the Atlantic Rain Forest of the State of São Paulo forms a distinct group from other regions and also from the interior region



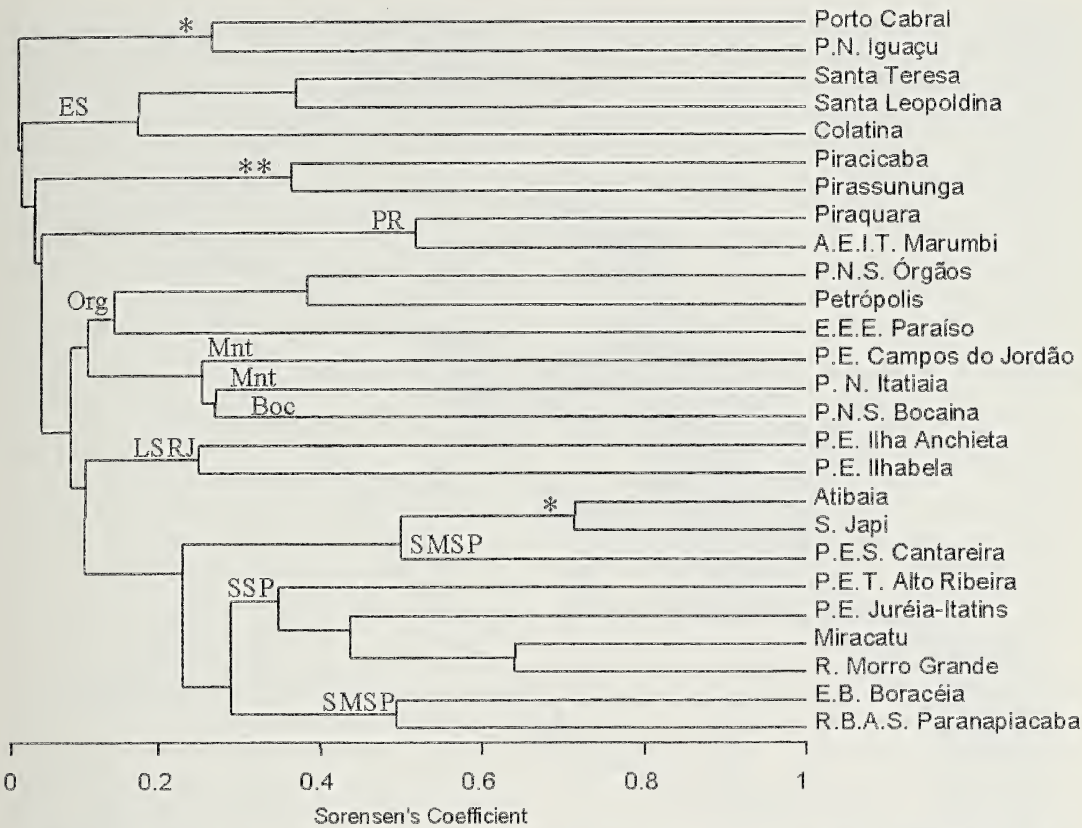


Figure 2.—Cluster analysis (Sørensen index) showing the similarity among harvestmen faunas (Lan- iatores and Eupnoi) of 26 areas in south and southern Brazil. Abbreviations in Table 1. \* = areas not included in biogeographic analyses; \*\* = Cerrado (savanna).

of São Paulo (Cantareira, Japi and Atibaia). This group is divided into a cluster from the southern coast of São Paulo (Miracatu, Juréia, Morro Grande and PETAR), and another in the center of the São Paulo Coastal Rain Forest (Boracéia and Paranapiacaba). A high similarity was found between the Serra do Japi (about 70%) and Atibaia, and can be explained by their proximity (ca. 30 km). The same occurs with the Paranapiacaba and Boracéia localities; besides their proximity, they belong to the same geomorphological formation. The fauna of the northern coast of the state of São Paulo is distinct from other regions of the State of São Paulo and even its two localities showed a low similarity (index below 0.30). It is possible to identify a great cluster composed of localities of Serra do Mar of Rio de Janeiro, Serra da Mantiqueira and Serra da Bocaina. Within this cluster, the localities are even distinctly different from each other, the Serra do Mar of Rio de Janeiro, including the

Serra dos Órgãos, formed a distinct subgroup from other localities, including Serra da Mantiqueira (Campos do Jordão and Itatiaia) and Serra da Bocaina. Other groups can be identified: localities of the cerrado (Piracicaba and Pirassununga); Serra do Mar of Paraná (Piraquara and Marumbi); Semi-deciduous Forest (P.N. Iguaçu and Porto Cabral); and a group formed by three localities in Espírito Santo. **Historical Biogeographic Analysis.**— Among the 84 species included in the analysis, 66 occur in one area, 13 were recorded in 2–3 areas, four in 4–8 areas and two have no precisely known locality (Table 1). The studied groups were not recorded in the cerrado and the more interior areas of the Atlantic Semi-deciduous Forest, except for the Mnt and the SEsp. Eleven areas of endemism were recognized as having at least three endemic species belonging to the subfamilies Caelopyginae, Goniosomatinae, Progonyleptoidellinae and Sodreaninae (Fig. 3). Primary BPA



Figure 3.—Strict consensus area cladogram of harvestmen subfamilies Caelopyginae, Goniosomatinae, Progonyleptoidellinae and Sodreaninae (Gonyleptidae) based on three equally parsimonious trees ( $L = 248$ ;  $CI = 0.66$ ;  $RI = 0.57$ ). Abbreviations of names in Table 1; \* = Paraíba do Sul River; \*\* = Ribeira do Iguape River.

analyses resulted in three equally parsimonious cladograms ( $L = 248$ ;  $CI = 0.66$ ;  $RI = 0.57$ ) and the strict consensus ( $L = 254$ ;  $CI = 0.64$ ;  $RI = 0.54$ ) is shown in Fig. 3. The three cladograms varied in positions of BA and SEsp, which formed a group in two cladograms, SEsp being more related to other areas than to BA in the third cladogram. The placement of Org and Mnt also varied, with the Org sister of Boc+LSRJ being in two cladograms and Mnt sister of the Boc + LSRJ in one. The consensus cladogram shows a sequence of vicariant events from North to South. However, it should be noted that the basal position of Bahia and Serra do Espinhaço in the cladogram could be due to the few

endemic species recorded in these areas besides the insufficient information to relate them to the southern areas, such as Serra do Espinhaço. The vicariant events that followed separated Espírito Santo from the southern areas and the central areas of São Paulo, and Rio de Janeiro from the southernmost areas. The Serra do Mar of the State of São Paulo was split from the continuous remaining part just south of São Paulo, as this area showed affinities with southern Brazil from which it is separated by the Ribeira do Iguape River.

#### DISCUSSION

Brazil harbors about 900 species of harvestmen (see Kury 2003 and Hallans catalog



at <http://entowww.tamu.edu/research/collection/hallan/OpilRpt2.txt>). The Coastal Atlantic Rain Forest possesses most of this diversity (about 600 described species), which makes this area the most diverse in the world for this taxonomic group. Among the 16 subfamilies of Gonyleptidae, the predominant group in the Atlantic Rain Forest, nine are exclusively found in this vegetation formation, whereas two occur mainly in this region (Tricommatinae and Hernandariinae). These 11 subfamilies include 223 described species. Other diversified groups found in this region are Pachylinae, Gonyleptinae and Sclerosomatidae, among others.

The study of similarity patterns (Fig. 2) among the well-sampled localities (Fig. 1) showed an almost total coincidence with the areas of endemism herein proposed. The very low similarity between localities and groups of localities show how isolated these faunas are. These results indicate the high influence of geomorphology and geographical isolation in the pattern of harvestmen species distribution. The clusters show, in general, that localities in the same mountain range are more similar to each other than to those in other mountain ranges.

There are two main biogeographic studies in South America that consider south and southeastern Brazil as belonging to more than one biogeographic component. Costa (1995) presented an area cladogram for three groups of Cyprinodontiformes, 23 other groups of fishes, and one genus of frog. Amorim & Pires (1996) presented a general area cladogram based on several groups of neotropical dipterans (Ditomyiidae, Sciaridae and Scatopsidae) and monkeys (Callitrichidae). Both hypotheses considered the Atlantic Rain Forest as having 4–6 components. However, the vicariant events postulated by these authors considered different areas of endemism for terrestrial and freshwater animals. Biogeography of the freshwater fauna seems to be related to paleodrainages that flowed to the interior or the Atlantic Ocean (Lundberg et al. 1998). On the other hand, the terrestrial fauna occurs on both sides of the mountain range. Costa (1995) suggested that the coastal areas form a component that is sister to a biogeographic component (his area “f”) that encompasses a large interior region around the La Plata and São Francisco Basins, and includes our area

BA. In his study, the components of the Serra da Mantiqueira and the Serra do Espinhaço do not possess any taxa. According to Costa (1995), the coastal components share a unique ancestral area in which the first vicariance event split areas “i+h” from “g” (similar to our areas SMSP, LSRJ, Boc, Org, and ES), followed by a second divergence between his areas “i” (with no taxon in our study), and “h” (our SC, PR e SSP). Amorim & Pires (1996) related SE Amazonia with other Brazilian regions. According to them, the areas comprising the center and northeast sections of Brazil (areas MGBA and NEBr in their fig. 26) form a component which is sister to southeast Bahia (our BA). This whole component is sister to a clade comprised of north Rio de Janeiro (our ES), São Paulo-Rio de Janeiro (our Org, Mnt, Boc, LSRJ, SSP, PR and SC), and southern Brazil and the northeast of Argentina (areas for which there are no opilionids related to this study).

The main vicariant events are related to mountain uplift and the appearance of valleys. The origin of the Serra do Mar and the Serra da Mantiqueira was during the Paleocene (Petri & Fulfaro 1988), or early in the Upper Cretaceous, as a result of tectonic activity (Almeida & Carneiro 1998). Although the great orographic ascension occurred between the Pliocene and the Pleistocene, we should stress the origin as being recent. Valleys seem to represent important geographical barriers, such as the valley of the Paraíba do Sul River, whose origin was during the Oligocene-Miocene (Petri & Fulfaro 1988), and isolated the Serra da Mantiqueira in the west from the Serra do Mar, Serra da Bocaina and the Serra dos Órgãos in the east. In addition, the same valley isolated the northern areas (Espírito Santo, Serra do Espinhaço and Bahia) from the remaining southern ones (Fig. 3).

It is interesting to note that the Atlantic side of most coastal mountains receives a large amount of rain (up to 4,000 mm a year). On the other hand, the interior side is in a rain shadow, and a valley such as Paraíba do Sul, receives one-third as much rain as the adjacent mountain range (Behling & Lichte 1997). Another remarkable fact was the generation of new environments during glaciations in the Pleistocene, such as grasslands and short gallery forests, in areas previously covered by rain forests, where currently there are semi-

Table 1.—Distribution of species of harvestmen subfamilies Caelopyginae, Goniosomatinae, Progonyleptoidellinae and Sodreaninae (Gonyleptidae) in eleven areas of endemism in south and southeastern Brazil. SC = Santa Catarina; PR = Paraná; SSP = Sul de São Paulo; SMSP = Serra do Mar de São Paulo; Mnt = Serra da Mantiqueira; Boc = Serra da Bocaina; LSRJ = north coast of São Paulo and south of Rio de Janeiro; Org = Serra dos Órgãos; ES = Espírito Santo; SEsp = Serra do Espinhaço; BA = southern coastal Bahia.

Species/area	SC	PR	SSP	SMSP	Mnt	Boc	LSRJ	Org	ES	SEsp	BA
Caelopyginae											
1. <i>Ampheres fuscopunctatus</i>				X			X				
2. <i>A. leucopheus</i>		X	X	X	X	X	X	X	X		
3. <i>A. luteus</i>					X						
4. <i>A. tocaninus</i>	?	?	?	?	?	?	?	?	?	?	?
5. <i>Arthrodes xanthopygus</i>								X			
6. <i>Caelopygus elegans</i>								X			
7. <i>C. melanocephalus</i>								X			
8. <i>Garatiba bisignata</i>							X				
9. <i>G. bocaina</i>						X					
10. <i>Metarthodes albotaeniatius</i>									X		
11. <i>M. bimaculatus</i>									X		
12. <i>M. hamatus</i>								X		X	
13. <i>M. laetabundus</i>						X		X			
14. <i>M. leucopygus</i>									X		
15. <i>M. longipes</i>				X			X				
16. <i>M. nigrigranulatus</i>					X	X		X			
17. <i>M. pulcherrimus</i>				X							
18. <i>M. xango</i>											X
19. <i>Metampheres albimargina-</i>											
<i>tus</i>								X			
20. <i>Pristocnemis albimaculatus</i>								X			
21. <i>P. farinosus</i>				X		X	X	X			
22. <i>P. perlatus</i>					X	X					
23. <i>P. pustulatus</i>		X	X	X	X	X	X	X			
24. <i>Thereza albiornata</i>									X		
25. <i>T. amabilis</i>							X				
26. <i>T. poranga</i>							X				
27. <i>T. speciosa</i>	X	X									
Sodreaninae											
28. <i>Gertia hatschbachi</i>		X									
29. <i>Sodreana sodreana</i>			X	X				X			
30. <i>Stygnobates barbiellinii</i>							X				
31. <i>Zortalia bicalcarata</i>								X			
32. <i>Z. inscripta</i>	X										
33. <i>Z. leprevosti</i>		X	X				X				
Progonyleptoidellinae											
34. <i>Cadeadoius niger</i>		X									
35. <i>Gonyleptoides acanthoscelis</i>								X			
36. <i>G. curvifemur</i>				X							
37. <i>G. marumbiensis</i>		X									
38. <i>Heliella singularis</i>		X									
39. <i>Iguapeia melanocephala</i>		X	X								
40. <i>Iporangaia pustulosa</i>			X								
41. <i>Leptocnema sulphurea</i>								X			
42. <i>Mitopernoides variabilis</i>							X				
43. <i>Moreiranula mamillata</i>				X							
44. <i>M. moreirae</i>					X						



Table 1.—Continued.

Species/area	SC	PR	SSP	SMSP	Mnt	Boc	LSRJ	Org	ES	SEsp	BA
45. <i>Progonyleptoidellus fuscop-</i> <i>ictus</i>				X							
46. <i>P. striatus</i>			X	X							
47. <i>Gen. sp.n. 1</i>							X				
48. <i>Gen. sp.n. 2</i>						X					
Goniosomatinae											
49. <i>Acutisoma banhadoae</i>		X									
50. <i>A. discolor</i>							X				
51. <i>A. hamatum</i>					X						
52. <i>A. indistinctum</i>										X	
53. <i>A. inerme</i>	X										
54. <i>A. inscriptum</i>							X				
55. <i>A. longipes</i>					X						
56. <i>A. molle</i>		X									
57. <i>A. proximum</i>		X	X	X							
58. <i>A. thalassinum</i>	X										
59. <i>A. sp.n. 1</i>		X									
60. <i>A. sp.n. 2</i>	X										
61. <i>A. sp.n. 3</i>			X								
62. <i>A. sp.n. 4</i>						X					
63. <i>A. sp.n. 5</i>				X							
64. <i>A. sp.n. 6</i>						X					
65. <i>A. sp.n. 7</i>											X
66. <i>A. sp.n. 8</i>					X						
67. <i>A. sp.n. 9</i>				X							
68. <i>Goniosoma albiscriptum</i>				X							
69. <i>G. calcar</i>								X			
70. <i>G. catarina</i>	X										
71. <i>G. dentipes</i>								X			
72. <i>G. ensifer</i>								X			
73. <i>G. modestum</i>											X
74. <i>G. roridum</i>								X			
75. <i>G. spelaeum</i>			X								
76. <i>G. unicolor</i>					X	X	X	X			
77. <i>G. vatrax</i>										X	
78. <i>G. venustum</i>								X			
79. <i>G. varium</i>								X	X		
80. <i>G. sp.n. 1</i>									X		
81. <i>G. sp.n. 2</i>								X			
82. <i>Gen n spn</i>							X				
83. <i>Lyogoniosoma macracan-</i> <i>thum</i>					X						
84. <i>Xulapona cara</i>										X	
Species/area	SC	PR	SSP	SMSP	Mnt	Boc	LSRJ	Org	ES	SEsp	BA
Total species	6	13	10	15	11	10	16	23	7	4	3
Endemic species	5	7	3	7	6	4	9	14	5	3	3

deciduous forests as in the interior of the State of São Paulo (Behling & Lichte 1997) or low-lands as is the case in the State of Santa Catarina (Behling & Negrelle 2001; Behling 2002). The replacement of rain forest by less

plant diverse and more open environments could have decreased the diversity of opilionids in those sites. The tree floras of semi-deciduous forests are less diversified than coastal forests, so they have been considered a

subgroup of the former (Oliveira-Filho & Fontes 2000). However, this difference is not as remarkable as it is in harvestmen. Nevertheless, we should stress that only two areas of the semi-deciduous forests were well sampled (Serra do Japi and Atibaia). This characteristic could lead to a misunderstanding of the relationships between coastal and interior areas. The high diversity of opilionids in the Coastal Atlantic Rain Forest, an area of higher diversity than any other country in the world, can be explained by the high number of geographical barriers on the Brazilian coast that isolated populations creating new species, and also by many events of forest fragmentation, hence leading to population divergence, due to climatic changes during the Pliocene-Pleistocene.

The unique opilionid faunas represented in each of the 11 areas of endemism call attention to the necessity of preserving those environments. The Atlantic Rain Forest is a hotspot, and the decimation of the Brazilian Atlantic Forest is one of the most alarming conservation problems in the world (Terborgh 1992). This biome possesses a great number of protected areas along the coast in the south-southeastern part of Brazil. In fact, most collecting was done in reserves. However, the opilionid faunas of three areas of endemism (ES, SEsp and BA) are poorly or not represented in terms of governmental reserves (see Conservation International do Brazil 2000 or the online atlas at <http://www.sosmatatlantica.org.br/?secao=atlas>), and their remaining habitats are suffering high anthropic pressure (Morellato & Haddad 2000), and deserve better attention in future planning of new protected areas in order to maintain the diversity of the group.

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## A SURVEY OF SPIDERS (ARANEAE) WITH HOLARCTIC DISTRIBUTION

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**ABSTRACT.** Of the 13,800 species distributed in the Holarctic Region only 395 are known both from Eurasia and North America. Of these only 105 species are distributed throughout the whole Holarctic (circum-Holarctic species). In addition, 28 species have an almost complete Holarctic distribution, occurring from Europe to northwestern North America (subcircum-Holarctic species). Species with a circum-Holarctic distribution were found in 13 families. The highest numbers of circum-Holarctic species were in the families Linyphiidae (37), Theridiidae (14), Araneidae (13) and Gnaphosidae (11). The percentage of the circum-Holarctic species among the Holarctic spiders is highest in Philodromidae (2.4%), Araneidae (2.2%), Theridiidae (2.0%) and Tetragnathidae (1.9%). These families encompass mainly herb-bush-tree dwellers. Somewhat unexpectedly it was found that most circum-Holarctic species occupy the boreo-nemoral zone (41%), or may even have a polyzonal range (23%). Twenty-nine species (28%) of the circum-Holarctic spiders have a northern distribution; most of them occurring both in arctic and boreal zones.

**Keywords:** Holarctic region, circum-Holarctic species, distribution types, zonal distribution, spiders

The Holarctic region, an area covering the Northern Hemisphere approximately north of 25° N, is the largest zoogeographical realm of the Earth. Around 13,800 species of spiders are listed in Platnick's (2004) catalogue as inhabitants of this realm. Without a doubt, the Holarctic is the best studied region in all groups of living organisms.

Most biogeographers divide the Holarctic region into two subunits, Palaearctic and Nearctic, lying in the Old and New World respectively. Among the species of spiders known in the Holarctic, only 395 species (or around 3%) are known from both Palaearctic and Nearctic regions. Most of them are listed in Platnick's (2004) and other catalogues as Holarctic or Cosmopolitan species.

Considering different meanings of the word Holarctic, we wish to stress that in this paper under the term Holarctic species (or distribution, range) or circum-Holarctic species (or distribution, range) we mean species occurring (distributed) throughout the whole or at least most of Eurasia and North America. Many authors consider distribution of species as Holarctic if they are known from two continents, although a species may be known only from one locality in one continent (e.g., Plat-

nick 2004). Holarctic species possibly introduced by man, long ago or more recently, have been treated here like the others, "naturally Holarctic" species.

The longitudinal width of the range of the circum-Holarctic species restricted to boreal or hypoarctic zones is slightly wider than that of species occurring in the nemoral zone (Figs. 1–2), although the real length (in kilometers) is longer in the nemoral zone. The nemoral zone starts in the Palaearctic at the Canary Islands (15°W) and continues to Kamchatka (160°E) (total length of the zone is about 180°); in the Nearctic this zone stretches from about 150°W (Alaska) to about 60°W (Nova Scotia) (length = 90°). Altogether the nemoral zone covers about 270°. The boreal and hypoarctic zones start at about 10°E (Fennoscandia) and continue almost without break to about 40°W (Greenland), and altogether comprise 310°. Species having polyzonal ranges or those that are synantropic have the widest ranges and can occur almost throughout the whole Holarctic.

The goal of this paper is to list all species of spiders which have a wide Holarctic range (either circum- or subcircum-Holarctic). Such a list can be a useful source for many fields



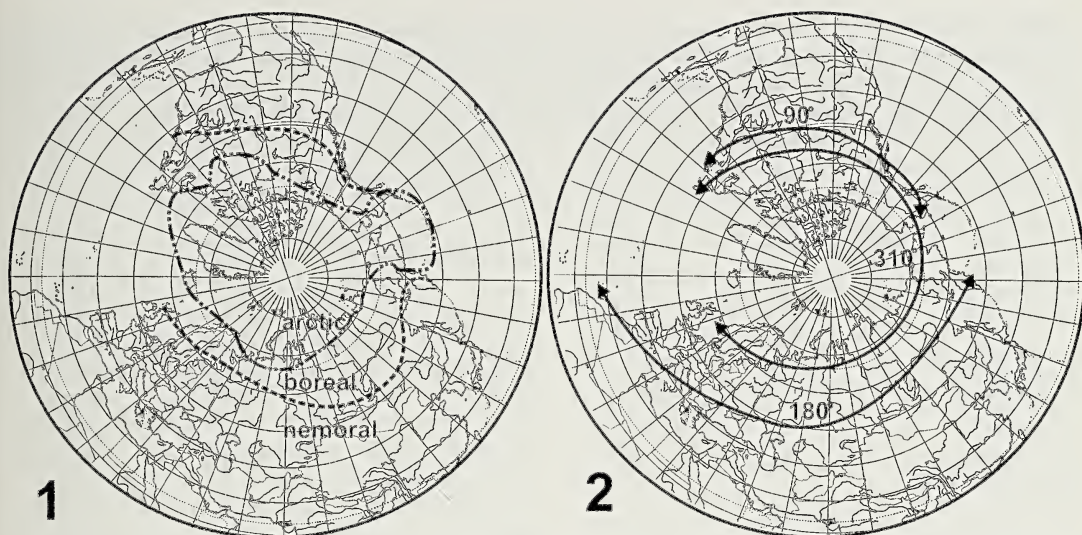


Figure 1-2.—1. Distributional zones in the Holarctic region. 2. The width of nemoral and boreal-hypoarctic zones in the Holarctic region.

of arachnology, like population genetics (variability across the wide range), ecology (comparative ecology and ethology of widespread species), taxonomy (morphological variation across the range), and physiology (study of cold resistance or thermal preferences in different parts of the wide range). Often comparative study, either ecological or morphological, on distant populations of widespread species reveals important differences which can lead to separation of new taxa.

#### METHODS

The major source of potential Holarctic species is the catalogue of Platnick (2004), from which the species mentioned as Holarctic were chosen. These species were studied using personal knowledge and recent species lists (e.g., Dondale et al. 1997; Marusik et al. 2000; Buckle et al. 2001). Many other publications have also been used, the most important are, in alphabetic order: Dondale & Redner (1990), Levi & Randolph (1975), Logunov (1996), Logunov & Marusik (2001), Marusik (1994), Marusik et al. (1992, 2002a, 2002b), Mikhailov (1997), Rybalov et al. (2002), Saaristo & Eskov (1996), Song et al. (1999) and Yoshida (2003).

The following main distribution types (abbreviations in brackets) have been distinguished (cf. Appendix 1): Arctic = tundra zone (ar); Boreal = taiga or coniferous forest

belt (bo); Hypoarctic = arctic + northern taiga + mountain tundra in boreal zone (hy); Nemoral = zone south of boreal: mixed or deciduous forest, steppe, desert (ne); Polyzonal = wide range within above types (po); Montane = mountains in nemoral zone (mo); Cosmopolitan (cos), see also Fig. 1.

#### RESULTS AND DISCUSSION

Of the more than 13,800 species recorded in the Holarctic Realm only 395 are known in both Eurasia and North America, and only 105 of them are distributed throughout the entire Holarctic, i.e. they are circum-Holarctic. In addition, 28 species have an almost Holarctic distribution, occurring from Europe to northwestern North America, i.e. they are subcircum-Holarctic. This means that less than 1% of all species in the Holarctic region are circum- or subcircum-Holarctic (Table 1). Thus, the number of truly Holarctic species of spiders is much lower than usually estimated (cf. Platnick 2004).

Of the 65 species listed as Holarctic in Prószyński & Staręga (1971) at least 16 are not really Holarctic. On the other hand, the number of species within the Holarctic has subsequently increased considerably due to active research in Siberia and the Nearctic (cf. Marusik et al. 2000). Marusik listed most of the present Holarctic species ten years ago (Ma-

Table 1.—Number of species found both in Nearctic and Palaearctic regions (1), number of species with circum- (2) and subcircum- (3) Holarctic distribution, percentage of circum-Holarctics of all species found in the Holarctic Realm (4), number of species found within the Holarctic Realm (5) and worldwide (6). Basic data from Platnick (2004). “Others” include Dysderidae, Hahniidae, Liocranidae, Miturgidae, Nesticidae, Oecobiidae, Oonopidae, Scytodidae, Sicariidae, Sparassidae, Theridiosomatidae, Uloboridae, and Zorapsidae.

Family	1	2	3	4	5	6
Agelenidae	7	1	—	0.3	295	490
Araneidae	23	13	—	2.2	599	2824
Clubionidae	10	3	—	1.2	259	529
Dictynidae	9	3	3	0.7	446	555
Gnaphosidae	27	11	—	0.9	1162	1955
Linyphiidae	160	38	13	1.3	3003	4247
Lycosidae	25	5	2	0.5	1041	2262
Philodromidae	15	7	2	2.4	286	512
Pholcidae	7	1	—	0.5	187	836
Salticidae	21	3	—	0.2	1382	4975
Tetragnathidae	7	3	—	1.9	160	1026
Theridiidae	45	14	5	2.0	690	2209
Thomisidae	15	3	1	0.5	609	2028
Amaurobiidae	3	—	1	—	444	626
Titanoecidae	1	—	1	—	34	46
Others	21	—	—	—	3189	13302
Total	395	105	28	0.8	13786	38432

rusik 1994); however, nine species have now been added and eleven omitted.

Species occurring both in the New and Old World parts of the Holarctic belong to 28 spider families (Table 1); however, species with circum-Holarctic distribution are known in 13 families only. Two additional families each have one subcircum-Holarctic species.

The following families have most Holarctic species: Linyphiidae (38), Theridiidae (14), Araneidae (13), Gnaphosidae (11), Philodromidae (7) and Lycosidae (5). The percentage of circum-Holarctic species among all the species found in the Holarctic Region, is highest in Philodromidae (2.4%), Araneidae (2.2%), Theridiidae (2.0%) and Tetragnathidae (1.9%) (Table 1). These families encompass mainly herb-bush-tree dwellers. Among genera, the most rich in circum-Holarctic species are *Micaria* (5), *Thanatus* (5) and *Theridion* (6). The last-mentioned genus seems to be paraphyletic, and its six species with circum-Holarctic range belong to three different groups.

We expected that, like in many other groups of living organisms (see Danks 1981), most of the species with a circum-Holarctic distribution would be restricted to the northern (boreal

and/or arctic) zones. The main reasons for this expectation were the smaller area and post-glacial history of the boreal, and especially the arctic zones, compared to the nemoral zone. However, it was found that most of circum-Holarctic species occur in the boreo-nemoral zone (41% or 43 species), and many even have a polyzonal range (23% or 24 species).

Among circum-Holarctic species, only 28% (or 29 species) have a northern distribution (arctic, hypoarctic and/or boreal range). Most of them occur both in tundra and boreal zones, and three species are known from the boreal zone only. Among the 28 subcircum-Holarctic species, as many as 16 (57%) have this kind of northern (arctic, hypoarctic and/or boreal) distribution pattern.

The proportion of cosmopolitans among circum-Holarctic species was highest in Theridiidae (4 species). Many species with a cosmopolitan range are absent from Siberia, like *Ostearius melanopygius* (O.P.-Cambridge 1879), *Tenuiphantes tenuis* (Blackwall 1852), *Diplocephalus cristatus* (Blackwall 1833), and two *Oecobius* species.

ACKNOWLEDGMENTS

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## Appendix 1.—Species with a circum- and subcircum-Holarctic range.

The distribution types used are: arctic (ar), boreal (bo), hypoarctic (hy), nemoral (ne), polyzonal (po), montane (mo) and cosmopolitan (cos), see also Methods. Species with a subcircum-Holarctic distribution have been marked with an asterisk (\*).

Agelenidae 1/0 (circum-Holarctic/subcircum-Holarctic)

*Tegenaria domestica* (Clerck 1757)—Cos.

Amaurobiidae 0/1

\* *Arctobius agelenoides* (Emerton 1919)—ar-bo, unknown in eastern half of the Nearctic.

Araneidae 13/0

*Aculepeira carbonarioides* (Keyserling 1892)—hy; *A. packardi* (Thorell 1875)—hy-ne; *Araneus diadematus* Clerck 1757—bo-ne; *A. marmoreus* Clerck 1757—bo-ne; *A. nordmanni* (Thorell 1870)—bo-ne; *A. saevus* (L. Koch 1872)—bo-ne; *Araniella displicata* (Hentz 1847)—bo-ne; *A. proxima* (Kulczyński 1885)—bo; *Cercidia prominens* (Westring 1851)—po; *Cyclosa conica* (Pallas 1771)—bo-ne, although absent in NE Siberia (east of Lena river); *Hypsosinga pygmaea* (Sundevall 1831)—po; *Larinioides cornutus* (Clerck 1757)—po; *L. patagiatus* (Clerck 1757)—po.

Clubionidae 3/0

*Clubiona kulczynskii* Lessert 1905—bo-ne; *C. pal-*

*lidula* (Clerck 1757)—bo-ne; *C. trivialis* C.L. Koch 1874—bo-ne.

### Dictynidae 3/3

\* *Arctella lapponica* (Holm 1945)—ar-bo, in Nearctic known only from the North-West; \* *Dictyna alaskae* Chamberlin & Ivie 1947—bo, in Nearctic is known from Alaska only; *D. arundinacea* (Linnaeus 1758)—po; *D. major* Menge 1869—po; *Emblyna annulipes* (Blackwall 1846)—bo-ne; \* *Hackmania prominula* (Tullgren 1948)—ar-bo, in Nearctic known only from the North-West.

### Gnaphosidae 11/0

*Gnaphosa microps* Holm 1939—hy-bo; *G. muscorum* (L. Koch 1866)—po, absent in NE Siberia and Far East; *G. orites* Chamberlin 1922—hy; *Haplodrassus signifer* (C.L. Koch 1839)—po; *Micaria aenea* Thorell 1871—bo-ne; *M. alpina* L. Koch 1872—hy-bo; *M. pulicaria* (Sundevall 1831)—bo-ne; *M. rossica* Thorell 1875—po; *M. tripunctata* Holm 1978—hy-bo; *Trachyzelotes jaxartensis* (Kroneberg 1875)—steppe-semidesert; *Zelotes puritanus* Chamberlin 1922—disjunctive polyzonal range, restricted to warm and xeric habitats from tundra zone to steppes and mountains.

### Linyphiidae 38/13

*Agyneta olivacea* (Emerton 1882)—hy-ne; \* *Allomengea scopigera* (Grube 1861)—bo-ne, in Nearctic restricted to the western half; *Aphileta misera* (O.P.-Cambridge 1882)—bo-ne; *Bathypantes gracilis* (Blackwall 1841)—bo-ne; *Caenorita linnaea* (Crosby & Bishop 1927)—bo; *Centromerus sylvaticus* (Blackwall 1841)—bo-ne; *Cnephalocotes obscurus* (Blackwall 1834)—bo-ne; *Collinsia holmgreni* (Thorell 1872)—hy-bo; *Diplocentria bidentata* (Emerton 1882)—bo-ne; *Diplocentria rectangulata* (Emerton 1915)—bo; *Dismodicus bifrons* (Blackwall 1841)—bo-ne; *Erigone arctica* (White 1852)—ar-bo-mo, represented by series of subspecies, none of which has Holarctic range; *E. atra* Blackwall 1833—po; *E. psychrophila* Thorell 1872—hy; *E. tirolensis* L. Koch 1872—hy (ar-mo); *Estrandia grandeva* (Keyserling 1886)—hy-ne; *Helophora insignis* (Blackwall 1841)—bo-ne; *Hilaira herniosa* (Thorell 1875)—hy-bo-mo; \* *H. nubigena* Hull 1911—bo, in Nearctic known from Alaska only; \* *Horcotes strandi* (Sytychevskaya 1935)—hy-bo, in Nearctic known from Yukon Territory only; \* *Hybauchenidium ferrumequinum* (Grube 1861)—hy, in Nearctic known from Yukon Territory only; \* *Hypselistes jacksoni* (O.P.-Cambridge 1902)—hy-ne, in Nearctic known only from Alaska to Utah; *Improphantes complicatus* (Emerton

1882)—bo-mo; \* *Islandiana falsifica* (Keyserling 1886)—hy, in Nearctic known from NW part (Alaska to Northwestern Territories, south to British Columbia); *Kaestneria pullata* (O.P.-Cambridge 1863)—bo-ne; "*Lepthyphantes*" *leprosus* (Ohlert 1867)—po, north of 55°N exclusively synantropic; *Macrargus multesimus* (O.P.-Cambridge 1875)—hy-ne; \* *Maso sundevalli* (Westring 1851)—bo-ne, in Nearctic known in Alaska only; \* *Mecynargus monticola* (Holm 1943)—hy-bo, in Nearctic known only from Western Canada only; *M. paetulus* (O.P.-Cambridge 1875)—bo-ne; *M. sphagnicola* (Holm 1939)—hy-bo, in Nearctic it occurs in Yukon and NW Territories; *Megalepthyphantes nebulosus* (Sundevall 1830)—po, north of 55°N exclusively synantropic; \* *Metopobatrax prominulus* (O.P.-Cambridge 1872)—bo-ne, in Nearctic known east of Saskatchewan; *Microlinyphia impigra* (O.P.-Cambridge 1871)—bo-ne; *M. pusilla* (Sundevall 1830)—po; *Microneta viaria* (Blackwall 1841)—po; *Neriene clathrata* (Sundevall 1830)—bo-ne; *N. radiata* (Walckenaer 1841)—bo-ne; *Oreonetides vaginatus* (Thorell 1872)—hy-bo-mo; *Pelelopsis mengei* (Simon 1884)—bo-ne; *Pocadicnemis pumila* (Blackwall 1841)—bo-ne; \* *Poecilometes variegata* (Blackwall 1841)—hy-bo-mo, in Nearctic restricted to the West; \* *Semljicola lapponicus* (Holm 1939)—hy, in Nearctic known from Alaska only; *Sisicus apertus* (Holm 1939)—bo-ne; *Thyreostenius parasiticus* (Westring 1851)—bo-ne; \* *Tibioplus diversus* (C.L. Koch 1879)—bo, in Nearctic known from Alaska and Yukon Territory; *Tiso aestivus* (L. Koch 1872)—hy-bo, in Nearctic known from Yukon Territory and Greenland; \* *Walckenaeria capito* (Westring 1861)—bo-ne, in Nearctic known from Ontario only; *W. cuspidata* Blackwall 1833—bo-ne; *W. karpinskii* (O.P.-Cambridge 1837)—ar-bo-mo; *W. lepida* (Kulczyński 1885)—bo-ne.

### Lycosidae 5/2

*Alopecosa aculeata* (Clerck 1757)—po; *Pardosa hyperborea* (Thorell 1872)—hy-bo, absent between Lena River and Alaska; \* *P. lapponica* (Thorell 1872)—hy-bo-mo, in Nearctic unknown west of the Hudson Bay; \* *P. palustris* (Linnaeus 1758)—bo-ne, in Nearctic known from Alaska, Yukon Territory and northern British Columbia; *Pirata piraticus* (Clerck 1757)—po; "*Tricca*" *alpigena* (Dolleschall 1852)—hy-bo-mo; *Trochosa terricola* Thorell 1856—bo-ne, in Siberia found only in areas free of permafrost, and rather rare in South Siberia.

### Philodromidae 7/2

*Philodromus cespitum* (Walckenaer 1802)—po; *P. rufus* Walckenaer 1826—bo-ne; *Thanatus arcti-*



*cus* Thorell 1872—ar-bo-mo (=?hy), in Siberia it has polyzonal range, in Scandinavia and Nearctic it is restricted to northern taiga and tundra; \* *T. coloradensis* Keyserling 1880—bo-mo, this species has disjunctions between Alps and Siberia (Marusik et al. 2000); *T. formicinus* (Clerck 1757)—bo-ne; *T. striatus* C.L. Koch 1845—po; \* *T. vulgaris* Simon 1870—ne (?), in Siberia it has disjunction between Xinjiang and Far East; *Tibellus maritimus* (Menge 1875)—bo-ne; *T. oblongus* (Walckenaer 1802)—bo-ne.

#### Pholcidae 1/0

*Pholcus phalangioides* (Fuesslin 1775)—Cos. In northern Palaearctic it is exclusively synantropic species, and most probably absent in South Siberia.

#### Salticidae 3/0

*Chalcoscirtus alpicola* (L.Koch 1876)—disjunctive hy-bo-mo range, in Eurasia known from Alps and Siberia east of Ural; *Salticus scenicus* (Clerck 1757)—bo-ne; *Sitticus ranieri* Peckham & Peckham 1909—hy-bo.

#### Tetragnathidae 3/0

*Pachygnatha clercki* Sundevall 1823—po; *Tetragnatha dearmata* Thorell 1873—bo-ne; *T. extensa* (Linnaeus 1758)—po.

#### Theridiidae 14/5

*Achaearanea tepidariorum* (C.L. Koch 1841)—Cos, in northern Holarctic it is a synantropic species; *Crustulina sticta* (O.P.-Cambridge 1861)—bo-ne; *Enoplognatha caricis* (Fickert 1876)—bo-ne; *Euryopsis saukea* Levi 1951—po (?), until 1972 it was known from the Nearctic and Poland

only. Later it was found in many places in Nearctic, Europe and Asia; \* *Neottiura bimaculata* (Linnaeus 1757)—bo-ne, in Nearctic known from British Columbia and Washington State; \* *Robertus lividus* (Blackwall 1836)—bo-ne, in Nearctic known from Alaska only; \* *R. lyriifer* Holm 1939—hy-mo, in Nearctic known from Alaska only; *Rugathodes aurantius* (Emerton 1915)—bo; *Steatoda albomaculata* (De Geer 1778)—po; \* *S. bipunctata* (Linnaeus 1758)—bo-ne, in Nearctic known from Ontario to Newfoundland; *S. grossa* (C.L. Koch 1838)—Cos, in northern Eurasia it is an exclusively synantropic species; *S. triangulosa* (Walckenaer 1802)—Cos; \* *Theridion impressum* L. Koch 1881—po, in Nearctic known from Alaska to western Northwest Territories and southward to northern Alberta; *T. montanum* Emerton 1882—bo-ne; *T. ohlerti* (Thorell 1870)—hy-bo-mo; *T. petraeum* L. Koch 1872—bo-ne; *T. pictum* (Walckenaer 1802)—bo-ne; *T. varians* (Hahn 1833)—bo-ne; *Theridula gonygaster* (Simon 1873)—Cos, in Palaearctic disjunctive distribution: in Asia known from Caucasus, Guangxi and Sichuan and Japan; in Nearctic known from Arizona and Florida.

#### Thomisidae 3/1

*Misumena vatia* (Clerck 1757)—po; \* *Ozyptila arcatica* Kulczyński 1908—hy-mo, in Nearctic known from Alaska to western Northwest Territories, south to northern British Columbia; *Xysticus luctuosus* (Blackwall 1836)—bo-ne; *X. obscurus* Collet 1877—bo-mo.

#### Titanoecidae 0/1

\* *Titanoeca nivalis* Simon 1874—bo-mo, in Nearctic restricted to the western half.

## FAUNA AND ZOOGEOGRAPHY OF SPIDERS (ARANEAE) IN BULGARIA

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**ABSTRACT.** Bulgaria is home to 975 species of spiders in 41 families. This number was established after a critical review of the existing literature and taxonomic review of the available collections. The spiders are distributed in all districts of Bulgaria, occurring in lowlands, forests, mountains, caves and urban territories. According to their current distribution the established 975 species can be split into 27 zoogeographical categories, grouped into five major chorotypes (Cosmopolitan, Holarctic, European, Mediterranean, Endemics). The largest number of species belongs to the widely distributed species in the Holarctic, but the most characteristic are the endemics. Their established number (76 species) is high and reflects the local character of the fauna. This phenomenon can be attributed to the relative isolation of the mountains compared with the lowlands in the context of paleo-environmental changes since the Pliocene.

**Keywords:** Europe, diversity, distribution, chorotypes

The first information on the spiders fauna of Bulgaria came from the end of 19<sup>th</sup> century (Pavesi 1876). Systematic investigation started in the beginning of 20<sup>th</sup> century by P. Drensky (1913, 1921, 1929, 1931, 1936a, b, 1937, 1938, 1939, 1940, 1942, 1943). Drensky (1936a) published the only catalogue of the spiders on the Balkan Peninsula in which 624 species from Bulgaria were reported. More recent publications are a result of intensive faunistic research after 1967 (Deltshhev 1967, 1972a, b, 1973, 1974, 1977a, b, 1978, 1980, 1983a, b, c, 1984, 1985, 1987a, b, 1988, 1990, 1992, 1993, 1996, 1997a, b, 1998, 2003; Deltshhev & Blagoev 1995, 1997, 2001; Helsingien et al. 1977 2001]; Blagoev & Deltshhev 1989; Blagoev et al. 2002; Dimitrov 1993, 1994, 1996, 1997, 1999, 2003; Dimitrov & Lazarov 1999, 2002; Thaler et al. 1994; Lazarov 1998, 2003, 2004; Lazarov et al. 2001; Tzonev & Lazarov 2001). The accumulation of new data makes possible a critical taxonomic and faunistic review, together with a zoogeographic analysis.

### METHODS

The material treated herein can be divided into two major parts: the first comprises a critical incorporation of all available literature records concerning the distribution of spiders in Bulgaria; the second concerns the original collections obtained from 1965–2002 during a field survey covering most of the districts in

Bulgaria, kept in the collections of Institute of Zoology, Bulgarian Academy of Sciences.

### RESULTS AND DISCUSSION

The spider fauna is represented in Bulgaria by 975 species, included in 41 families and 285 genera. The number of species is high compared with the number of spiders recorded from other European countries with similar territories (Tables 1, 2). The number of families is also high compared with the data for the world: 110 (Platnick 2005; Austria 40, Germany 39, Switzerland 39 (Blick et al. 2002). Best represented are the families Linyphiidae (226 species or 23.2%), Gnaphosidae (98 species or 10%), Salticidae (91 species or 9.3%), Lycosidae (80 species or 8.2%) and Theridiidae (74 species or 7.5%). The genera with the highest number of species are: *Centromerus* (16 species or 7.3%), *Walckenaeria* (14 species or 6.4%), *Tenuiphantes* (11 species or 5%) and *Diplocephalus* (9 species or 4.1%) (Table 2). This richness, however, depends not only on the size of the regions, but also on the degree of exploration by araneologists.

According to their current distribution Bulgarian spiders can be divided into 27 zoogeographical chorotypes, grouped into 5 zoogeographical complexes (I = Cosmopolitan, II = Holarctic, III = European, IV—Mediterranean, V = Endemic) (Fig. 1). The data concerning general distribution of spiders are tak-



Table 1.—Comparison of area and spider species richness of some European countries.

Country	Area (km <sup>2</sup> )	Spider species	Sources
Austria	83,858	961	Blick et al. (2002)
Bulgaria	110,993	975	Blagoev et al. (2002)
Czech Republic	77,280	830	Buchar & Růžička (2002)
Greece	128,900	810	Bosmans (pers. comm.)
Hungary	92,340	725	Samu & Szinetar (1999)
Macedonia	25,713	558	Blagoev (2002)
Portugal	91,500	660	Cardoso (1999)
Serbia	102,000	618	Deltshev et al. (2003)
Slovenia	20,120	529	Kuntner & Šereg (2002)

en from Michailov (1997), Marusik et al. (2000), Platnick (2004) and Vigna Taglianti et al. (1999) (Fig. 1).

*Cosmopolitan species complex (COS + SCO, 20, 2%)*: Includes especially widespread species associated with lowlands, woodlands and high elevation zones of mountains.

*Complex of species widely distributed in the Holarctic Region (HOL + OLW + PAT + PAL + WPA + ECA + EEC + SEC + EEE + WPA)*: Is best represented and comprises 561 (57.5%) species widespread in Bulgaria (Fig. 1). Palearctic species (sensu lato) are dominant (36.1%), followed by Holarctic (10.5%), European Central Asiatic (7%) and

West Palearctic (3%). The remaining chorotypes (EEC, SEC & EEE) are represented by single species. The complex includes especially widespread species associated with lowlands, woodlands and high elevation zones of mountains. Most of the species are well represented in the mountains. Characteristic mountain species are represented by the linyphiids *Bolyphantes alticeps* (Sundevall 1833), *B. luteolus* (Blackwall 1833), *Frontinellina frutetorum* (C. L. Koch 1834), *Gonatum rubens* (Blackwall 1833), *Pityohyphantes phrygianus* (C. L. Koch 1836), *Tenuiphantes alacris* (Blackwall 1853), *T. tenebricola* (Wider 1834). High mountain species are the lin-

Table 2.—The spider fauna of Bulgaria listed by families, depicting numbers of genera and species.

Families	Genera	Species	Families	Genera	Species
Atypidae	1	2	Oxyopidae	1	3
Nemesiidae	2	4	Zoropsidae	1	2
Filistatidae	2	2	Zoridae	1	6
Scytodidae	1	1	Agelenidae	6	32
Leptonetidae	1	2	Cybaeidae	2	3
Pholcidae	4	7	Hahnidae	4	9
Segestridae	1	3	Dictynidae	8	15
Dysderidae	4	29	Amaurobiidae	5	22
Oonopidae	4	4	Titanoecidae	2	7
Mimetidae	2	4	Miturgidae	1	12
Eresidae	1	2	Anyphenidae	1	2
Oecobiidae	1	1	Liocranidae	7	13
Uloboridae	2	4	Clubionidae	1	26
Nesticidae	1	3	Corinnidae	3	5
Theridiidae	17	74	Zodariidae	1	11
Theridiosomatidae	1	1	Gnaphosidae	19	96
Linyphiidae	94	226	Sparassidae	2	3
Tetragnathidae	4	17	Philodromidae	4	32
Araneidae	16	56	Thomisidae	13	60
Lycosidae	11	80	Salticidae	31	91
Pisauridae	2	3			
			Total	285	975

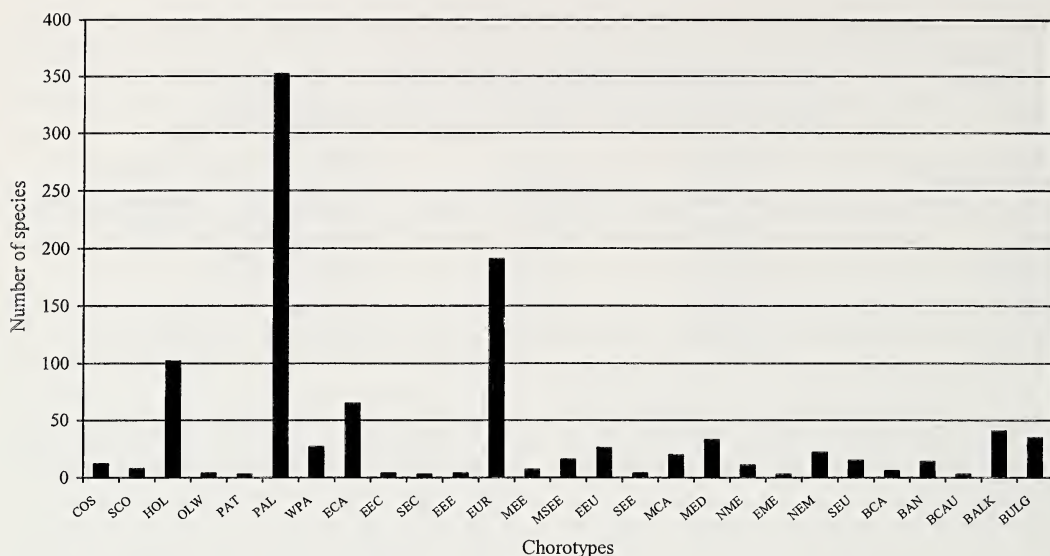


Figure 1.—Zoogeographical types in the spider fauna of Bulgaria, showing the number of species represented in each. Abbreviations: COS = cosmopolitan; SCO = subcosmopolitan; HOL = Holarctic; OLW = Old World; PAT = Palearctic-Paleotropical; PAL = Palearctic; WPA = west-Palearctic; ECA = European-central Asian; EEC = east European-central Asian; SEC = south European-central Asian; EEE = east European-east Mediterranean; MCA = Mediterranean-central Asian; BCA = Balkan-central Asian; EUR = European; MEE = middle-east European; MSEE = middle-southeast European; SEU = south European; EEU = east European; SEE = southeast European; BCAU = Balkan-Caucasian; BAN = Balkan Anatolian; MED = Mediterranean; EME = east Mediterranean; NME = north Mediterranean; NEM = northeast Mediterranean; BALK = Balkan endemics; BULG = Bulgarian endemics.

lyphiids *Entelecara media* (Kulczyński 1887) and *Mecynargus paetulus* (O.P.-Cambridge 1875), which are not established in the forest belt. Some xenotopic species (Thaler 1988) are widely distributed in the mountains and reach the highest summits as aeronauts. To this group belong the linyphiids *Dicymbium nigrum* (Blackwall 1834), *Diplostyla concolor* (Wider 1834), *Meioneta rurestris* (C.L. Koch 1836), *Oedothorax agrestis* (Blackwall 1853), *O. apicatus* (Blackwall 1850), *O. fuscus* (Blackwall 1834) which inhabit the mountain zone in dense populations (Deltshev 1990, 1995).

**European species complex (EUR + MEE + MSEE + EEU + SEE):** Comprises 191 (20%) species, widespread in Europe and Bulgaria (Fig. 1). European species (sensu lato) are dominant (14%), followed by East European species (3%), and Middle Southeast European species (1.5%). The remaining chorotypes (MEE & SEE) are represented by single species. The complex comprises widespread species which inhabit both lowland and mountains. Interesting is the group of European

mountain species, best represented in the forest, subalpine and alpine belts. Characteristic mountain species are the linyphiids, *Araeoncus anguineus* Deltshev 1987, *Bolyphantes kolosvaryi* (Caporiacco 1936), *Cinetata gradata* (Simon 1881), *Diplocephalus foraminifer* (O.P.-Cambridge 1875), *Improphantes improbulus* (Simon 1929), *Maso gallicus* Simon 1894, *Mughiphantes pulcher* (Kulczyński 1881), *Oreonetides glacialis* (C.L. Koch 1872), *Tiso vagans* (Blackwall 1834). Other linyphiid species such as *Palliduphantes istrianus* (Kulczyński 1914), *Centromerus capucinus* (Simon 1884), *C. cavernarum* (L. Koch 1872), *Porrhomma lativellum* Tretzel 1956 and *P. microps* (Roewer 1931), are characteristic of caves.

**Mediterranean species complex (MCA—MED + EME + NME + NEM + SEU + BCA + BAN + BCAU):** Includes 127 species (13%) that occur in the Mediterranean area or a part of it. The complex forms only 13% of the total spider fauna of Bulgaria, but the real percentage is probably higher, because a large part of the endemics have a Mediterranean or-



igin. Most of the species in the complex are widely distributed in the Mediterranean region. Very interesting are the mountain-Mediterranean species [*Aculepeira talishia* (Zavodsky 1902), *Pardosa incerta* 1905], which may be regarded as ancient elements in the high mountains.

*Endemic species complex (BALK + BULG)*: Includes 76 species (10%) established in Bulgaria (35 species) and other territories of the Balkan Peninsula (41 species). The established number is high and reflects the local character of the fauna. The question about the status and distribution of endemic spiders found in Bulgaria is complicated. Some of them are found only in restricted areas, while others show wider distributions, sometimes even over the whole peninsula.

According to their origin, the endemics form two groups. Some of the species can be regarded as probable remnants of ancient Mediterranean mountain fauna (paleoendemics), and others came from the northern parts of Europe during the glacials and evolved under isolation on mountains during the interglacials (neoendemics). The curious is the distribution of the genus *Antrohyphantes* Dumitrescu 1971 (Linyphiidae), found only in the high elevation zone and in caves. It is related to the genus *Fageiella* Kratochvíl 1934 (Linyphiidae), an endemic from the caves of the western part of the Balkan Peninsula (Bosnia, Montenegro). Their allopatric distribution indicates that they had already separated before the establishment of the Vardar tectonic zones (Deltshev 1996). This suggests that these two genera are paleoendemics.

Concerning the formation of cave fauna, Deeleman-Reinhold (1976) wrote that "many European cave spiders are probably relics of populations of moist Tertiary forests". Due to the lack of knowledge, it is difficult to determine with certainty which of the cave spider endemics of Bulgaria are Tertiary and which are Quaternary elements. Nevertheless, the blind species in the family linyphiid, *Centromerus bulgarianus* (Drensky 1931), *Troglohyphantes drenskii* Deltshev 1973 and *Troglohyphantes bureschianus* Deltshev 1975, all species with primitive three branched paracymbia, also can be regarded as probable paleoendemics (Deltshev 1996).

The linyphiid spiders *Araeoncus clivifrons* Deltshev 1987, *Diplocephalus altimontanus*

Deltshev 1984, *Drepanotylus pirinicus* Deltshev 1992, *Erigone l. pirini* Deltshev 1983, *Incestophantes annulatus* (Kulczyński 1882), *Mughiphantes lithoclasticolus* Deltshev 1983, *Metopobactrus orbelicus* Deltshev 1985, known only from the high alpine parts of the Pirin and Rila Mountains are high alpine elements?. Here, also can be placed *Thenuiphantes drenskyi* Helsdingen 1977, occurring in the high elevation belts of Pirin, Rila, Central Stara Planina and Vitosha mountains. These species are regarded as derivative of their respective North or Middle European species (*Diplocephalus picinus* (Blackwall 1841), *Drepanotylus borealis* Holm 1945, *Erigone longipalpis* (Sundevall 1830), *Metopobactrus prominulus* (O.P.-Cambridge 1872), due to the disjunction of ranges during the glacial and interglacial (Deltshev 1996; Deltshev & Blagoev 1997). The largest fraction of endemics was encountered mainly in caves, coastal sites, woodlands and high altitude zones.

The presence of the 975 spider species shows that Bulgaria is a territory of considerable species richness. This conclusion is supported also by the existence of 76 endemic species. In a zoogeographical respect, the widely distributed spiders in the Holarctic region are dominant. However, the most characteristic faunal elements are the endemics. Their number is high, and their faunistic composition reflects the local character of the fauna. According to their origin the endemics belong to two principal faunistic complexes: Mediterranean and European. This phenomenon can be explained by the relative isolation of the mountains compared with the lowlands, in the context of palaeo-environmental changes that have occurred since the Pliocene.

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## GEOGRAPHICAL CONTEXT OF SPECIATION IN A RADIATION OF HAWAIIAN *TETRAGNATHA* SPIDERS (ARANEAE, TETRAGNATHIDAE)

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**ABSTRACT.** Adaptive radiation involves the diversification of species each adapted to exploit different ecological roles. I have studied a radiation of spiders in the genus *Tetragnatha* (Tetragnathidae) in the Hawaiian Islands to elucidate processes involved in such diversification. The temporal framework of the Hawaiian Islands allows examination of the changing pattern of adaptive radiation over time, as lineages have generally progressed down the island chain from older to younger islands. Species of *Tetragnatha* in the spiny-leg clade on any one island are typically most closely related to others on the same island, and the same set of ecological forms (ecomorphs) has evolved repeatedly on different islands. These results indicate that adaptive radiation frequently involves ecological divergence between sister taxa to allow multiple close relatives to co-occur in the same habitat. The current study examines the geographical context within which these species arose. I focus on a clade of 5 species that occur on the volcano of East Maui; at any given site 3 species can co-occur, one of each of 3 different ecomorphs. Mitochondrial DNA sequences from populations of these 5 species from throughout their distribution (Maui, Lanai and Molokai) were used to infer the geographic history of the species on East Maui and to determine whether diversification likely occurred *in situ*, or alternatively whether diversification occurred in allopatry on different volcanoes. Although ecological differentiation between taxa is evident, allopatry is clearly implicated in the initial divergence of taxa. Further study is required to understand the nature of the interplay between allopatry and ecological divergence in species formation.

**Keywords:** Adaptive radiation, biogeography, allopatry, parapatry, evolution

One of the most hotly debated aspects of the speciation process is its geographical context, and the nature and importance of isolation in the initial divergence of taxa (Coyne & Orr 2004). As a result of the influential work of Mayr (1963), ideas of speciation were dominated for many years by the importance of allopatry in initiating divergence (Coyne 1994; Howard & Berlocher 1998). However, theoretical studies have demonstrated that sympatric speciation can occur and can cause species to form much more rapidly than by allopatric speciation (Turelli et al. 2001; Gavrillets 2003). The importance of sympatric speciation in nature, however, remains questionable (Coyne & Orr 2004). Recent studies on species and speciation have started to recognize the validity of some of the predominant ideas of the earlier part of this century, including the role of both divergent natural selection (Schluter 2001) and hybridization (Seehausen 2004) in generating new species. In particular, ecological speciation, in which reproductive isolation evolves as a conse-

quence of divergent natural selection on traits between contrasting environments, is now recognized as an important mechanism of speciation (Schluter 2001). However, the geographic context of speciation in situations of adaptive radiation, where multiple close relatives occur in sympatry, is still the subject of considerable debate (Glor et al. 2004).

The current study focuses on the Hawaiian Islands, the most isolated archipelago in the world and well known for some of the most extraordinary illustrations of adaptive radiation (Simon 1987; Wagner & Funk 1995). The Hawaiian island chain is a hotspot archipelago, arranged in chronological series, the youngest island being Hawaii, the oldest Kauai (Carson & Clague 1995; Price & Clague 2002). The biogeographic pattern that predominates in most Hawaiian taxa, both species and populations, is a step-like progression down the island chain from the oldest to the youngest islands (Wagner & Funk 1995), often with repeated bouts of diversification within islands (Roderick & Gillespie 1998).

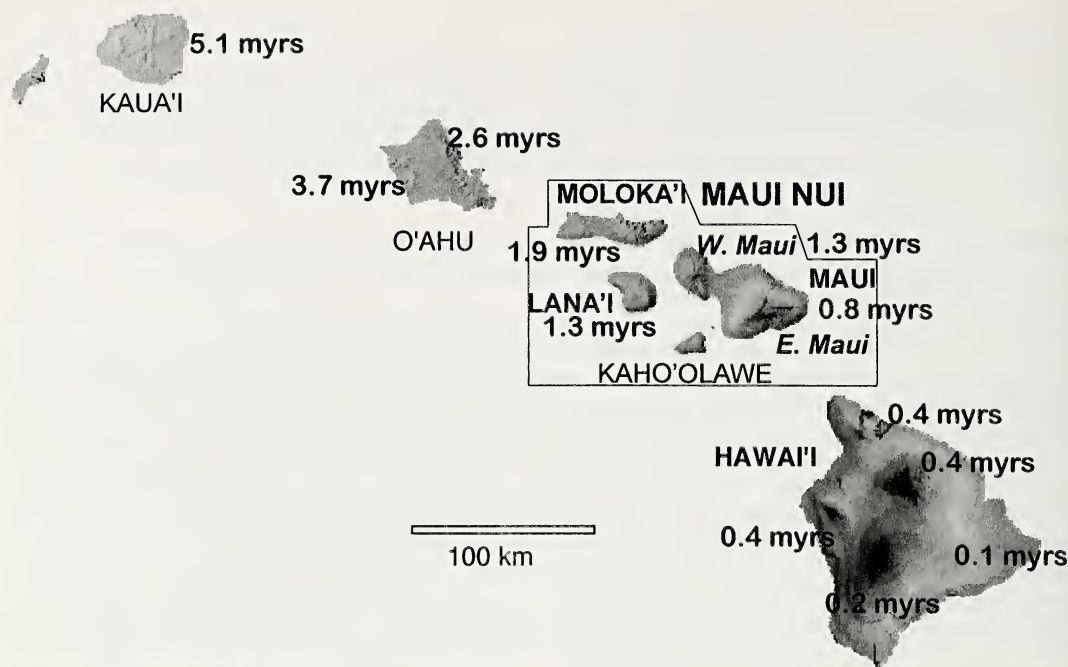


Figure 1.—Map of the Hawaiian Islands. Names in bold type indicate islands that were the focus of the current study. Ages of the different volcanoes are given (myrs = million years).

Accordingly, the islands are considered a “natural laboratory” as they allow study of patterns of species formation on islands of different age (Gillespie 2004, 2005). Here, I focus on an adaptive radiation in the spider genus *Tetragnatha* (Tetragnathidae) in the Hawaiian Islands to examine the geographic context involved in the initial divergence of taxa.

The genus *Tetragnatha* is strikingly diverse in the Hawaiian Islands, with multiple species occurring in sympatry throughout the islands. Until 1991, only 8 species had been described from the islands. Over the last few years I have described an additional 29 species of Hawaiian *Tetragnatha* (Gillespie 1991, 1992a, 1994, 2002, 2003) and am currently describing approximately 15 more species. This species radiation encompasses forms representing a huge spectrum of colors, shapes, sizes, ecological affinities and behaviors. Many species are web builders, with their shapes modified to allow concealment within specific microhabitats (Blackledge & Gillespie 2004). Some species have modifications of the jaws, apparently to allow specialization on specific prey types (Gillespie 2005). However, several groups have abandoned the characteristic

web-building behavior of the genus (Gillespie 1991, 1992b). For example, one entire clade, or lineage, of 16 species (the “spiny leg” clade), has “lost” web building behavior, with the concomitant development of long spines along the legs and adoption of a vagile, cursorial, predatory strategy.

Recent studies have shown that representatives of the spiny leg clade occur as four distinct ecomorphs associated with specific habitat types: “green spiny” on leaves; “maroon spiny” on moss, “large brown spiny” on tree bark, and “small brown spiny” on twigs (Gillespie et al. 1994; Gillespie et al. 1997). Similar sets of ecomorphs occur in most native habitats and phylogenetic analyses have shown that ecomorphs have arisen repeatedly and independently (Gillespie 2004). In particular, the most ubiquitous ecomorph, *green spiny*, has evolved (or been lost) at least once on each of the older islands, Kauai (*T. kauaiensis*), Oahu (*T. tantalus*, *T. polychromata*), and Maui Nui, the once connected volcanoes of Molokai, Lanai, and Maui (*T. brevignatha*, *T. macracantha*, *T. waikamoi*). Likewise, the *maroon spiny* has evolved independently on Oahu (*T. perreirai*) and Maui Nui (*T. kamakou*); both species are



closely related to species of the *green spiny* ecomorph. Also, one of the small *brown spiny* ecomorphs (*T. restricta*) has evolved independently on Maui. The island of Hawaii, presumably because it is still very young, contains mostly populations of the same species that occur on Maui (Gillespie 1991).

The distribution of ecomorphs across habitats is significantly different from random (Gillespie 2004): there is a remarkably similar representation of ecomorphs in different habitats. Not all habitats have all ecomorphs, but there is never more than one representative of a given ecomorph at a site. The finding that similar ecomorphs never co-occur is most striking on East Maui. Here, a representative of each ecomorph is found at almost every site on the volcano, yet the species composition of the array of four different ecomorphs changes quite markedly between different locations (Gillespie 2005). Different species of the same ecomorph have very clear cut parapatric distributions. Moreover, different ecomorphs that co-occur are frequently sister species, suggesting the possibility that ecological differences may have arisen *in situ*. However, populations of these species also occur on other volcanoes, suggesting a potential role for allopatry in the initial divergence of taxa.

Here, I focus on a group of sympatric species to determine how divergence may have occurred within the geographic context of the Maui Nui island complex. Specifically, I examined 5 species that are found on East Maui: *T. kamakou* (*maroon spiny*), *T. restricta* (*small brown spiny*), and *T. waikamoi*, *T. macracantha*, and *T. brevignatha* (*green spiny*). (The *large brown* ecomorph is represented at all sites by *T. quasimodo*, but this species falls outside the clade of 5 species which form the focus of the current study). *Tetragnatha kamakou* and *T. restricta* co-occur with each other and with one of the green spiny ecomorphs (*T. waikamoi*, *T. macracantha*, or *T. brevignatha*) at different locations on the volcano. The question addressed here is whether species in the Maui Nui clade formed through diversification within the single volcano of East Maui or alternatively whether divergence occurred in allopatry, prior to their current distribution.

## METHODS

**Study Sites and Organisms.**—The study was focused on the more recent part of the

Hawaiian archipelago, Maui Nui and Hawaii (Fig. 1). Maui Nui is a composite of 4 separate islands, Maui, Molokai, Lanai, and Kahoolawe. Until 300,000–400,000 years ago, these islands were all connected, much like the island of Hawaii is today (Carson & Clague 1995). Glacially mediated fluctuations in sea level have alternately flooded and exposed the land connecting islands of the complex of islands. Except for Kahoolawe, all islands of Maui Nui have been sufficiently high to maintain native forest. Each island has a single high volcano except for Maui itself, which has two. These volcanoes range in age from Molokai (1.8 MY), through Lanai and West Maui (1.3MY) to East Maui (0.8MY). The island of Hawaii is the largest in the archipelago and the youngest. It consists of 5 volcanoes, the oldest being Kohala (0.43MY), then Hualalai (0.40MY), Mauna Kea (0.38MY), Mauna Loa (0.20MY), and Kilauea (0.10MY).

The five focal species for the study were *T. brevignatha*, *T. macracantha*, *T. kamakou*, *T. restricta*, and *T. waikamoi*. Specimens collected from different sites are shown in Table 1.

As outgroups, I used two populations of *T. quasimodo*, East Maui, Waikamoi, Carruthers, 6100ft, 26 June 1994; and Hawaii, Puu Maaka, 11 July 1994.

**Phylogenetic Hypotheses.**—An approximately 730 base pair piece of Cytochrome oxidase subunit I (COI) was amplified using primers LCO-1628 (ATAATGTAATTGT-TACTGCTCATGC) and HCO-2396 (ATTGT-AGCTGAGGTAAAATAAGCTCG) (Palumbi 1996). Genbank accession numbers are given in Table 1. Historical hypotheses of phylogenetic relationships were reconstructed using three methods: (i) Maximum Parsimony as the optimality criterion in the program PAUP\* version 4.0b10 (Swofford 2000). Heuristic searches were performed by step-wise addition of taxa, with TBR branch swapping and 1000 step-wise random taxon addition replicates. Characters were weighted (transversions: transitions) 2:1. Of the total characters: 543 characters were constant, 143 variable characters were parsimony-informative, and 44 characters were parsimony-uninformative. (ii) Maximum Likelihood as the optimality criterion. MODELTEST v. 3.04 (Posada and Crandall 1998), which makes use of log likelihood scores to establish the model of DNA evolution that best fits the data, was first





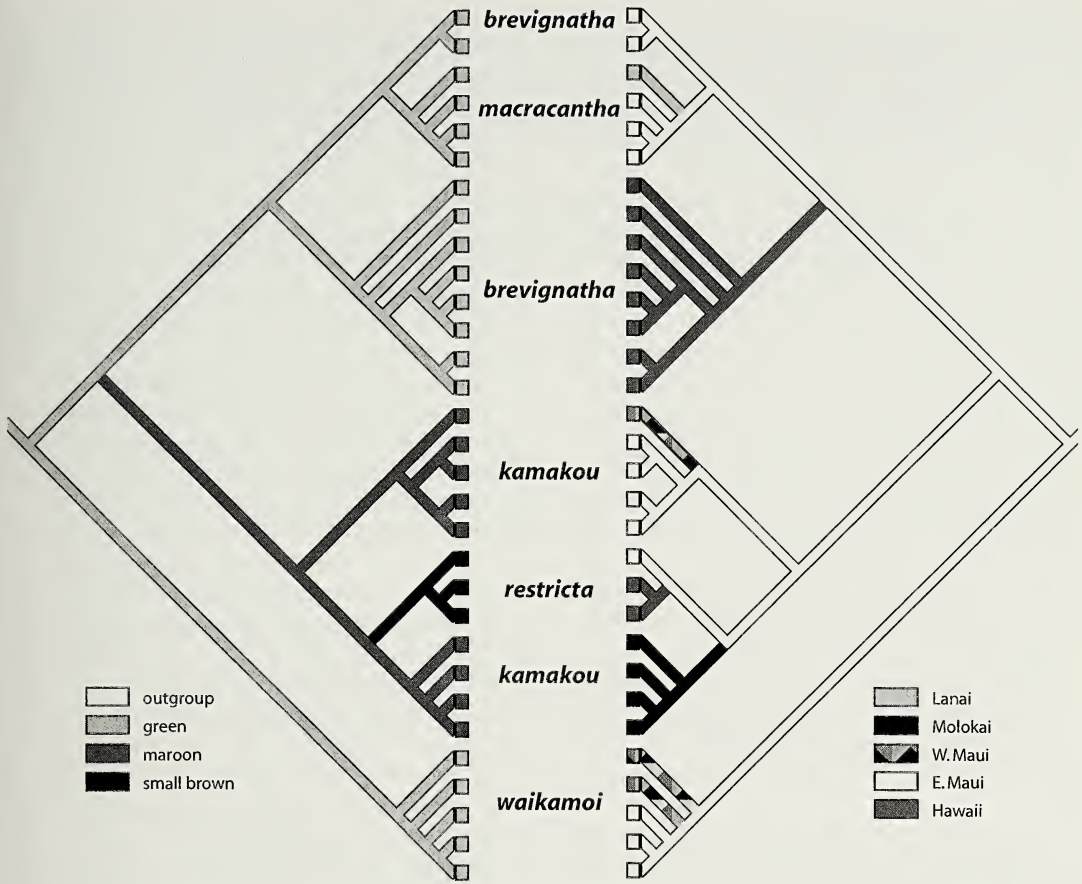


Figure 3.—Ancestral state reconstruction to infer transformations in ecomorph category and island (or volcano within island). Ecomorph category and island affiliation were mapped on to the molecular phylogeny using the accelerated transformation (ACCTRAN) optimization.

used to determine parameter values. The HKY85+G+I model was selected: negative log likelihood, 3381.6406, and Akaike Information Criterion (AIC), 6775.2812. This is a general time-reversible model of DNA substitution with a gamma distribution for the rate of substitution at a site and a shape parameter gamma distribution of 1.4870. The proportion of invariable sites (I) was estimated as 0.612. The base frequencies were estimated as: A, 0.2586; C, 0.1650; G, 0.2058; T, 0.3705 with a ti/tv ratio of 2.9285. (iii) Bayesian Inference of Likelihood with posterior probability of phylogenies approximated by sampling trees from the posterior probability distribution. The program MrBayes (Huelsenbeck 2000) uses Markov chain Monte Carlo (MCMC) to sample phylogenies according to their posterior probabilities, with the marginal probability of trees calculated from the trees visited

during the course of the MCMC analysis. The proportion of the time any single tree is found in this sample is an approximation of the posterior probability of the tree. The estimates from MODELTEST were used as priors for the Bayesian inference of phylogeny using MrBayes 3.0. MacClade 4 (Maddison and Maddison 2000) was used to overlay ecomorph category on the molecular phylogeny and determine the most parsimonious scenario for ecomorph evolution. Both accelerated and delayed transformation optimization options were applied.

RESULTS

Phylogenetic estimation using Maximum Parsimony, Maximum Likelihood and Bayesian Inference gave a similar topology (Fig. 2). Support for nodes, which was provided by bootstrap support for Maximum Parsimony

and Maximum Likelihood and Posterior Probabilities for the Bayesian Inference of Likelihood, was generally high. Geographical locations were mapped against the tree topology to determine probable ancestral geographic affinities for each species/ population. The results gave strong support for the following clades: “brevignatha Maui”; “brevignatha Hawaii”; “all macracantha Maui + Lanai”; “kamakou Maui”; “kamakou Molokai”; “all restricta Maui + Hawaii”; and “all waikamoi Maui”. There was also strong support for the clade “restricta + only kamakou Molokai”; this renders *T. kamakou* paraphyletic with respect to *T. restricta*. Most importantly, however, it suggests that, although *T. restricta* (Maui + Hawaii) co-occurs with *T. kamakou* on Maui, and *T. kamakou* is the sister species of *T. restricta*, the population of *T. kamakou* which is sister to *T. restricta* is not on Maui, but on Molokai, another volcano in the Maui Nui group of islands.

There was weak support for a clade of “brevignatha Maui” + “macracantha Maui + Lanai”, which, if upheld, would render *T. brevignatha* paraphyletic relative to *T. macracantha*.

The character reconstructions to examine the evolution of ecomorphs are shown in Fig. 3, using ACCTRAN, which minimizes parallel evolution. The topology indicates that a minimum of 3 character transformations are required, one with the divergence of *T. kamakou* from *T. brevignatha* + *T. macracantha*, the second with the divergence of *T. restricta* from *T. kamakou* Molokai. Also, based on the reconstruction, E. Maui appears to be the ancestral geographic locality, although this may be because E. Maui, with by far the largest land mass in the island complex, has the largest number of species and thus is the island most likely to have haplotypes represented across the tree.

## DISCUSSION

Throughout the native forest on the volcano of Haleakala, East Maui, four species of spiny leg *Tetragnatha* can co-occur, and when they do, only one of each of the primary ecomorphs is found in any given location: *green spiny* (*T. waikamoi*, *T. brevignatha*, or *T. macracantha*), *maroon spiny* (*T. kamakou*), *small brown spiny* (*T. restricta* or *T. kikokiko*), and *large brown spiny* (*T. quasimodo*). In this pa-

per I focused on five species of Hawaiian *Tetragnatha* that form a Maui Nui clade and are each others' closest relatives (Gillespie 2004): *T. waikamoi*, *T. brevignatha*, *T. macracantha*, *T. kamakou*, and *T. restricta*. *Tetragnatha kamakou*, and *T. restricta* co-occur with *T. waikamoi*, *T. brevignatha*, or *T. macracantha* throughout their distribution. The predominant ecomorph and the ecomorph represented by the most number of species, is *green spiny*, with *T. waikamoi* being sister to the remaining species in the clade, and *T. brevignatha* and *T. macracantha* forming sister species.

Previous work has shown that different species of *green spiny* never co-occur (Gillespie 2004, 2005), suggesting that ecological divergence between taxa might involve some degree of isolation. The results presented here do not reject the hypothesis that isolation plays a role in the divergence of sister species of the same ecomorph. For example, the green spiny *T. macracantha* (from East Maui and Lanai) is monophyletic and sister to the East Maui population of green spiny *T. brevignatha*. However, because *T. macracantha* has a population on Lanai as well as East Maui, it is possible that divergence between these two taxa occurred in allopatry.

The most informative result comes from the clade including *T. kamakou* and *T. restricta*, which is sister to the clade comprising *T. brevignatha* and *T. macracantha*. In particular, the mitochondrial tree shows that East Maui populations of *T. kamakou* and *T. restricta*, which occur in sympatry throughout much of the volcano, are each more closely related to populations on other volcanoes: for example, *T. restricta* is most closely related to *T. kamakou* from Molokai and individuals of *T. kamakou* on East Maui are most closely related to individuals of *T. kamakou* on West Maui. One explanation for this pattern could be colonization of Hawaii by *T. restricta*, divergence in allopatry, and subsequent recolonization of Maui. However, given the tendency of taxa to colonize from older to younger islands, and not the reverse (Wagner & Funk 1995), this scenario would be unusual. A second scenario is suggested by the reconstruction of historical geographical areas (Fig. 3), which indicates that *T. restricta* diverged from *T. kamakou* on East Maui, with *T. kamakou* going on to colonize Molokai. However, it is difficult to suggest a process that might lead



Table 1.—Taxonomic and geographical information of the specimens included in the present study including GenBank accession numbers for COI sequences for each specimen. \*, Genbank Accession Number. Collectors: MA, M. Arnedo; GB, Greta Binford; LB, Lindell Bromham; CE, Curtis Ewing; RG, Rosemary Gillespie; MH, Mandy Heddle; AM, A.C. Medeiros; GO, Geoff Oxford; DP, Dan Polhemus; MR, Malia Rivera; GR, George Roderick; KS, Kerry Shaw; AT, AnMing Tan.

Species	Volcano	Locality	Elev.	Date	Collector	Code	Genbank*
<i>T. brevignatha</i>	E. Maui	Waikamoi, Fence	4400ft	21 October 1995	RG,MH,MA,MR	J70	DQ182752
	E. Maui	Waikamoi, Nr Flume	4400ft	9 November 1996	RG	GJ86	DQ178958
	Mauna Loa	Kipuka at mile 18	5000ft	9 March 1995	RG	D95	DQ182753
		Kipukas	5050ft	13 June 2002	RG,GR	14.1JG	DQ182754
		Kahua Ranch	3780ft	11 June 2002	RG,GR	Tet2	DQ182756
<i>T. macracantha</i>	Kohala	Koloko Dr.	3200ft	12 June 2002	RG,GR	Tet8	DQ178961
	Hualalai	Kealakekua	3740ft	9 March 1990	RG	Tet1	DQ178959
	Mauna Loa	Puu Makaala	4300ft	11 July 1994	GB	11.2JG	DQ182755
	Kilauea	Kipahulu	4000ft	15 May 1990	RG,AM	J52	DQ182765
	E. Maui	Kipahulu	3000ft	16 May 1990	RG,AM	J53	DQ182766
<i>T. kamakou</i>		Kaumakani	3700ft	7 June 1999	CE, DP	Tgs1	DQ182767
	Lanai	Munro Trail	3300ft	20 June 1999	MA	Tgs2	DQ182768
	E. Maui	Waikamoi, Carruthers	6150ft	17 November 1992	RG	GJ81	DQ182760
		Waikamoi, Nr Flume	4400ft	9 November 1996	RG	GJ72	DQ178963
		Kaumakani	3700ft	7 June 1999	CE, DP	TTk2	DQ182761
<i>T. restricta</i>	W. Maui	Puu Kukui	4550ft	13-1-98	RG, KS	TTk1	DQ182762
	Molokai	Puu Lua	3180ft	15 June 1999	MA	Tgs3	DQ182759
		Puu Lua	3180ft	15 June 1999	CE, DP	00006	DQ178962
		Puu Lua	3180ft	15 June 1999	CE, DP	Tet6	DQ182758
	E. Maui	Waikamoi, Fence	4200ft	3 July 1993	RG	GJ74	DQ182763
<i>T. waikamoi</i>	Mauna Kea	Hakalau, Maulua Tr.	6000ft	17 June 1999	RG, GR, LB	73	DQ178964
	Mauna Kea	Hakalau, Maulua Tr.	6150ft	16 August 1997	RG	J35	DQ182764
	E. Maui	Waikamoi, Nr Flume	4200ft	3 July 1993	RG	00012	DQ182771
		Hanawi	5000ft	6 May 1998	CE	TTw1	DQ182770
		Waikamoi Flume	4300ft	27 February 1993	RG	GJ28	DQ182769
<i>T. quasimodo</i>	W. Maui	Puu Kukui	4550ft	13 August 1994	GS, AT	J28	DQ178965
		Puu Kukui	4550ft	13 January 1998	RG, KS	00009	DQ182772
	E. Maui	Waikamoi, Carruthers	6100ft	26 June 1994	RG		AY490287
	Kilauea	Puu Makaala	4300ft	11 July 1994	GB		AY490308

to such an inferred sequence of events. Finally, a third scenario is that the divergence of *T. restricta* from *T. kamakou* was initiated by colonization from the older Molokai. For example, if East Maui were occupied by *T. kamakou* and the volcano was subsequently colonized a second time by *T. kamakou* from Molokai, disruptive selection could lead to the formation of a new, ecologically differentiated species. This final scenario of an older ancestor is also supported by the inferred time of divergence between *T. restricta* and *T. kamakou*: The maximal uncorrected pairwise genetic divergence between these species is 9.1 %, an amount which, when scaled to a global arthropod rate of mitochondrial sequence divergence of 2.3% per million years (Brower 1994), minimally dates the ancestor to 1.98 MYA, the approximate age of Molokai. However, if *T. restricta* diverged from *T. kamakou* Molokai before E. Maui was formed 0.8MYA (Fig. 1) as the dating suggests, the geographical context of the divergence remains enigmatic, as *T. restricta* has not been found on any island older than E. Maui. Further sampling of populations and genetic loci may help resolve this issue.

The results also indicate that both *T. brevignatha* and *T. kamakou* are paraphyletic when considering populations on the different volcanoes: *T. brevignatha* (E. Maui + Hawaii) with respect to *T. macracantha* (E. Maui + Lanai) and *T. kamakou* (W. Maui + E. Maui) with respect to *T. restricta* (E. Maui + Hawaii). Paraphyly at the species level is not uncommon (Funk & Omland 2003), and may even be expected under the scenario of ecological speciation. Among island radiations, the phenomenon has been clearly demonstrated in species of beetles (Rees et al. 2001) and lizards (Thorpe et al. 1994) in the Canary Islands and also a radiation of anole lizards in the Caribbean (Thorpe & Stenson 2003). In the current study, *T. restricta* has clearly emerged within *T. kamakou*: all extant allopatric populations of *T. kamakou* are very similar morphologically and do not warrant distinct species status.

One limitation of the current study is that it is based entirely on mitochondrial DNA sequences. Mitochondrial gene trees can frequently conflict with species trees, generally as a result of unsorted ancestral variation (lineage sorting) or hybridization (Rokas et al.

2003). Among Hawaiian arthropods, studies of both flies (*Drosophila*) and crickets (*Laupala*) have shown marked differences between trees generated from nuclear DNA versus mitochondrial DNA. For example, interspecific hybridization has been a regular occurrence in the history of both *Drosophila* (DeSalle & Giddings 1986) and *Laupala* (Shaw 2002; Mendelson & Shaw 2005). However, for the Hawaiian *Tetragnatha*, there is no evidence that hybridization between species occurs regularly. Considerable work on the phylogenetic relationships among the species considered here based on nuclear loci (allozymes and minisatellites) (Pons & Gillespie 2003, 2004; Gillespie 2004) shows no evidence of unsorted historical variation or recent introgression between any of the species or populations within species. Thus, we can assume that the mitochondrial data do accurately represent the phylogenetic history of the species examined in the current study. That *Tetragnatha* do not hybridize, despite the young age of many species, is interesting in comparison with *Drosophila* and *Laupala*: In both the flies and crickets, sexual selection has been implicated as a major force in driving speciation (Kanehiro 1989; Shaw & Herlihy 2000). By contrast, sexual selection appears not to play such a key role in Hawaiian *Tetragnatha* (Roderick & Gillespie 1998); rather, ecological affinities appear to be of greater significance in the initial stages of differentiation. Although still largely conjecture at this point, ecological affinity may play a key role in reinforcing isolation of gene pools in *Tetragnatha*, a process that perhaps is not as important in *Drosophila* and *Laupala*.

Together with previous studies on the spiny leg clade (Blackledge & Gillespie 2004; Gillespie 2004), the results of the current study suggest that there is a strong ecological component to species diversification. These results corroborate similar findings that have appeared in the literature for other adaptive radiations. In particular, extensive within-habitat proliferation, and repeated evolution of similar ecomorphs in different habitats has been found in cichlid fish in the Great African Lakes (Ruber et al. 1999), sticklebacks in Canadian glacial lakes (Schluter & McPhail 1993; Schluter 1998; Schluter 2000), and *Anolis* lizards in the Caribbean (Losos et al. 1998). In most of these cases, species pairs



appear to have had an allopatric phase in their recent history (e.g., threespine sticklebacks and Darwin's ground finches). The only exception in which no allopatric phase is indicated is that of the *Rhagoletis* flies (Feder et al. 1988; Filchak et al. 2000), although even here the possible role of allopatry cannot be ruled out (Coyne & Orr 2004). The radiation of Hawaiian *Tetragnatha* suggests, as do results from studies of many other adaptive radiations, that allopatry, together with ecological divergence, plays an important role in the formation of species. Future studies on the interplay between divergence in allopatry and ecological differentiation will be critical to understanding the mechanism of speciation within an adaptive radiation.

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## DIVERSITY OF ARBOREAL SPIDERS IN PRIMARY AND DISTURBED TROPICAL FORESTS

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**ABSTRACT.** This study investigates how arboreal spider communities in SE-Asian primary lowland rain forests change after anthropogenic disturbance. Two types of secondary forests were distinguished: 1) forests adjacent to each other, which finally merged into primary forest and 2) forests that were isolated by at least 10 km from the primary forest. Three forests of different age were investigated from each type and compared with undisturbed primary forest. All disturbed forests had been used some years for agriculture and were then left between 5 and 50 years to regenerate naturally. Spiders from at least seven trees per forest type were collected using insecticidal knockdown fogging and sorted to species or morphospecies level. Spiders represented between 5–10% of all canopy arthropods. A similar number of spiders were collected per square meter from all trees. However, communities in the primary forest differed greatly in their alpha- and beta-diversity and in community structure from those in the disturbed forest types. Diversity was high in the regenerating forests connected to the primary forest and approximated the conditions of the primary forest during the course of forest succession. In contrast, the isolated forests were of low diversity and communities showed little change during forest regeneration. These results indicate the importance of a species-source from which disturbed forests can be recolonized. However, even under optimal conditions this process needed decades before spider communities became similar to those of the primary forest. With no species-source available, spider diversity changed little during 50 years of forest regeneration. In the isolated forest we observed a drastic turnover from forest species towards species characteristic of open vegetation and shrubs. Our results give an indication of how large a loss in diversity can be expected in isolated forest fragments.

**Keywords:** Fogging, fragmentation, forest isolation, recolonization, species-source

The canopy of tropical lowland rain forests forms a highly complex habitat. Here lives the most diverse arthropod fauna of the world, which influences many ecosystem processes and ecosystem services (examples in Linsenmair et al. 2001; Basset et al. 2003). This assessment has been based on the faunistic-ecological analysis of taxa such as Coleoptera, Lepidoptera or Formicidae (e.g., Erwin 1983; Morse et al. 1988; Floren et al. 2001, 2002; Brehm et al. 2003; Davidson et al. 2003) while comparatively little work has been done on other groups. However, these latter groups can be rich in species and of great ecological importance, such as Araneae (Hoefer et al. 1994; Deeleman-Reinhold 2001; Santos et al. 2003) which, next to Formicidae, are the most abundant predators in the trees (Stork 1991; Floren & Linsenmair 1997; Wagner 1997). Despite political declarations, tropical forests are recklessly destroyed and reduced to forest

fragments which are much simpler in species diversity and habitat complexity. Although this destruction will certainly change many ecosystem properties, the consequences of this transformation have never been adequately investigated. This study aims at providing such knowledge. We investigated the diversity and structure of arboreal spider communities in SE-Asian primary forests. Furthermore, we analyzed how communities differ in disturbed forest types and how they reorganized following anthropogenic disturbance. We collected arboreal spiders by insecticidal knockdown fogging. Besides primary forest, we studied 1) three secondary forests of different ages that merged into each other and finally into primary forest and 2) three isolated secondary forests of different ages which were separated by at least 10 km from the primary forest. This study design allowed us to assess the importance of species recolonization for the re-

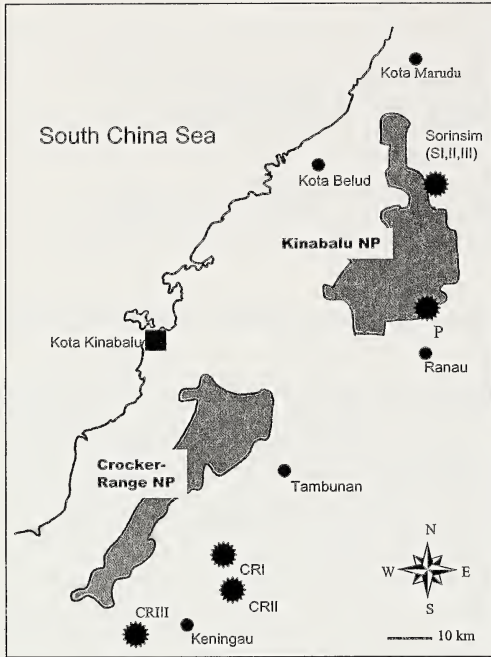


Figure 1.—Map of study sites. SI, SII, SIII were adjacent forests of 5, 15, and 40 years age that merged into primary forest at Kinabalu National Park substation Sorinsim. CRI, CRII, CRIII, were isolated forest plots of 10, 20, and 50 years age that were at least ten kilometers away from the primary forest. P = primary forest plots.

organization of spider communities during forest regeneration. After eight years of taxonomic analysis by the senior author we are now able to present the results of our investigation.

## METHODS

**Study sites.**—Arboreal arthropods were collected by insecticidal knockdown fogging in a Dipterocarp lowland rain forests of Kinabalu National Park (500–650 meters a.s.l.) in Sabah, Malaysia on Borneo ( $6^{\circ} 2.75'N$ ,  $116^{\circ} 42.2'E$ ) during various field periods from 1992–2001 (Table 1). The area has a relatively constant climate with a main rainy season from November to February and a shorter one from June to July. The level of precipitation varies between 2000 and 4000 mm. In total, 15 trees of the genus *Aporosa* (Euphorbiaceae) were fogged, 6 trees of *Xanthophyllum affine* (Polygalaceae) and 9 trees of various other genera (for details see Horstmann et al. in press). The disturbed forests were situated at substation Sorinsim in Kinabalu National

Park and in the vicinity of the Crocker Range National Park. A map of all forest types is shown in Fig. 1. Details on the study sites are published elsewhere (Floren et al. 2001; Horstmann et al. in press). All secondary forests were clear-cut for crop planting, abandoned and left for natural regeneration. Three forests of 5, 15 and 40 years, each of 5–6 ha (abbreviated SI, SII, SIII), which merged into one another and finally into primary forest, were investigated at National Park substation Sorinsim. Foggings were carried out from February–March 1997. Three isolated forest plots of 10, 20 and 50 years were found within at least 10 km distance from the primary forest of the Crocker Range National Park (abbreviated CRI, CRII, CRIII). They were about 4–6 hectares in size and surrounded by cultivated land (fruit, oil palm, rubber plantations, pastures, etc.). Fieldwork was carried out between January and February 2001. All disturbed forests had only a single canopy layer which was in no case closed and differed both in tree height and girth at breast height of the study trees.

**Collecting methods.**—A full description of the fogging method is given in Adis et al. (1998). Natural pyrethrum was used as an insecticide and all arthropods that dropped into the collecting funnels two hours following fogging were used in the analysis. In order to collect arboreal arthropods as completely as possible, 80–90% of a crown projection area was covered with collecting funnels installed beneath a tree. In total, 102 foggings were carried out, consisting of the first and subsequent foggings (mostly on consecutive days). Faunistic analysis is based on all these foggings while only the first foggings were used for community level analysis (Table 1). Seven primary forest trees were re-fogged after three years and two trees after an eight month period. Spider communities from these samples could not be distinguished from those of the first foggings and were, therefore, considered independent samples. As no tree species grew in all forests, a common tree was fogged in each forest type. However, as tree specific associations of broad-leaved trees are thought to be of minor importance for spiders and were also not indicated by our results, we refer to Floren & Linsenmair (2001) for the general discussion of this aspect. Analysis is based on



Table 1.—Forests investigated and focal trees. Individual trees were refogged several times on consecutive days. SI, SII, SIII = secondary forests connected with primary forests; CRI, CRII, CRIII = isolated secondary forests.

Focal tree species		Number of foggings		Tree height (m)	Girth in breast height (cm)
		Fog 1	Re-fog		
Primary forest	<i>Aporosa lagenocarpa</i>	27	3	24–30	70.24 ± 18.12
	<i>A. subcaudata</i> (Euphorbiaceae)				
SI (5 yrs.)	<i>Melochia umbellata</i> (Sterculiaceae)	8	10	6–8	57.91 ± 9.46
SII (15 yrs.)	<i>Vitex pinnata</i> (Verbenaceae)	11	4	18–20	106.44 ± 14.54
SIII (40 yrs.)	<i>V. pinnata</i>	10	5	20–25	148.44 ± 48.14
CRI (10 yrs.)	<i>Melanolepis glandulosa</i> (Euphorbiaceae)	8	—	6–8	83.16 ± 9.89
CRII (20 yrs.)	<i>M. glandulosa</i>	7	—	18–20	107.43 ± 14.54
CRIII (50 yrs.)	<i>M. glandulosa</i>	9	—	18–25	122.89 ± 23.20

adult spiders, which are stored in the collection of C. Deeleman.

**Data analysis.**—Spider communities in forest types were compared using alpha- and beta diversity indices (Magurran 1988). William’s alpha (after Fisher et al. 1943) is a widely used parametric index of diversity, which is largely independent of sample size. Simpson’s index describes the probability that a second individual drawn from a population should be of the same species as the first. It is mainly influenced by common species and therefore a measure of equitability (the larger the value the greater the equitability). Sample sizes were standardized by using rarefaction statistics (Hurlbert 1971; Hayek & Buzas 1997). For this purpose, spiders of all fogged trees per forest type were pooled and diversity was expressed as the number of expected species within an equal sub-sample size (this corresponded with the 65 species identified from all 306 specimens in the isolated forest CRI). If rarefaction values are computed for increasing sub-samples and plotted graphically, the resulting curve can be interpreted as a species accumulation curve, which gives information on the structure of spider communities in each forest type (Achtziger et al. 1992). Shinozaki curves were calculated to compare communities on the beta-diversity level (Shinozaki 1963; Achtziger et al. 1992). They are expected species accumulation curves based on qualitative (presence / absence) data of species. Their steepness provides information about the overall completeness of the sampling effort. Furthermore, Soerensen’s quantitative index of similarity was calculated. Dif-

ferences in means of beta-diversity between forest types were tested with a Mantel test using a randomization test (Monte Carlo). The number of randomized runs was 1000. For a between forest comparison, the fogging data were standardized for a crown projection of 1m<sup>2</sup> and a leaf cover of 100%.

RESULTS

From all 102 foggings, 6999 spiders were collected and sorted to 578 species in 29 families (Appendix 1). Scientific names were found for 107 species of which 75 species (12.9%) were new for Borneo. The five most abundant families, declining in rank-order, were Theridiidae, Salticidae, Araneidae, Thomisidae, and Clubionidae, together representing between 73% and 94% of all spiders in each forest. These families contributed also between 75% and 84% of all species. Theridiidae represented 153 species, Salticidae 111 species, Araneidae 80 species, Thomisidae 74 species, and Clubionidae 31 species. Spiders provided on average between 4.6% and 9.8% of all arthropods in a community (Table 2). Differences in the relative proportion of spiders per tree were detected only between the youngest isolated forest CRI and the primary forest, CRI and SII, and CRI and SIII (ANOVA, *F* = 4.235, *df* = 6, *P* < 0.01, Tamhane post-hoc tests for unequal variances were carried out, *P* < 0.05). The number of collected spider individuals, standardized on 1m<sup>2</sup> collecting sheets and 100% leaf cover, differed not significantly between tree species or forest types, only between the primary forest and SII where spider numbers were lowest (ANOVA,

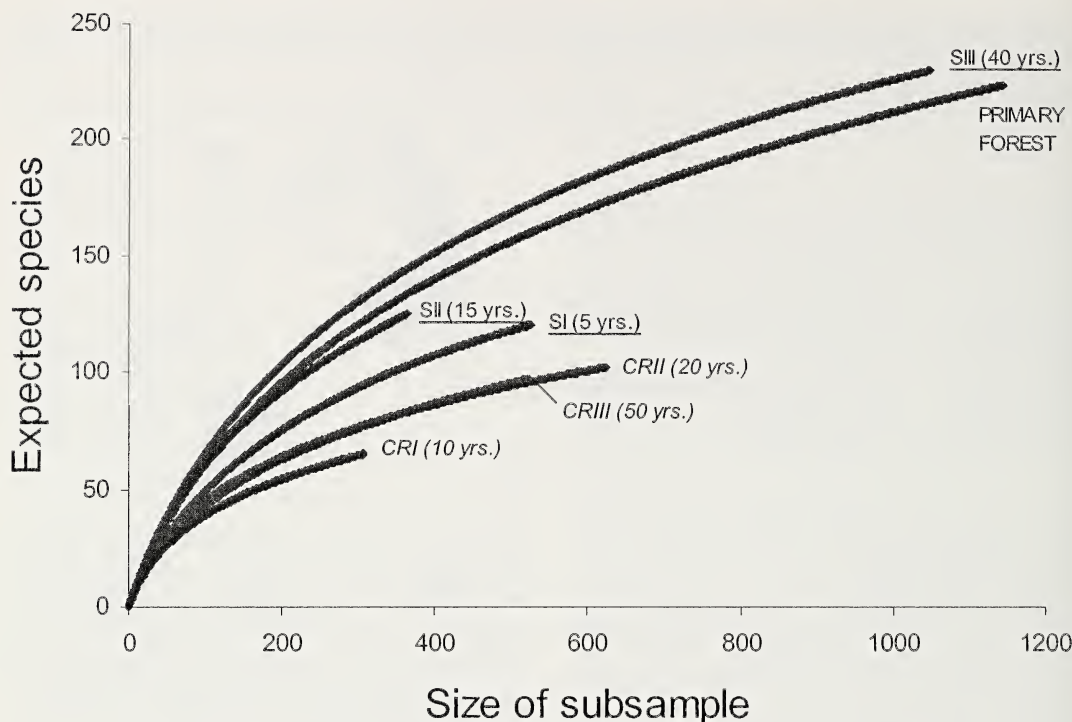


Figure 2.—Rarefaction curves of spider communities based on all foggings.

$F = 2.358$ ,  $P < 0.05$ , Tamhane post-hoc test,  $df = 6$ ,  $P < 0.05$ ). Most abundant in the forests close to the primary forest was *Talaus nanus* (Thorell 1892) (Thomisidae) with 297 individuals, followed by *Ogulinus* sp. (Theridiidae) with 103 individuals, and *Molione kinabalu* (Yoshida 2003) (Theridiidae) with 74 individuals. The isolated forests were numerically dominated by *Ocyllus* sp. (Thomisidae) with 75 individuals followed by *Tetragnatha hasselti* (Thorell 1890) (Tetragnathidae) with 51 specimens. Family diversity depended on sample size and was highest in the primary forest. Rarefaction statistics allow comparison of forest types that have been sampled with different efficiency. On a rarefied sub-sample of 306 individuals (corresponding to the number of spiders of the smallest sample CRI) a similar number of families, namely 22, were observed in SII and the primary forest. The number of spider families was least in the isolated forest plots. Rarefied species numbers and, correspondingly, William's alpha were highest in the primary forest and in SIII. Again these indices were clearly lower in the isolated forests where alpha-diversity had changed little even after 50

years compared to the 'Sorinsim-forests'. Rarefied species numbers were higher both in SI and SII than in CRI and CRII (related to the gradient forests these were 30.9% and 33.0%, respectively), and 41.7% more species were collected in SIII compared to CRIII. An approximate value for the loss of species following anthropogenic disturbance is the relation of species numbers to primary forest species numbers (Floren & Linsenmair 2005). Only 22.0% of the primary forest species number was collected in the isolated forest CI, the most severely disturbed forest with the lowest number of species. Relative proportion of singletons in each forest type was lowest in the primary forest (32.4%) and increased in the disturbed forests. Despite the large sampling effort in the primary forest, there were still 96 species represented by only one individual. In contrast to the proportion of singletons per forest type, the mean proportion of singletons of all tree specific communities per forest type was a better discriminator between primary and disturbed forests despite high variance between tree specific communities. The average proportion of singletons was highest and not significantly different in the primary and the



old secondary forest SIII (Table 2). The primary forest (mean  $25.8 \pm 11.8$ ) differed from the isolated forests CRI (mean  $10.3 \pm \text{SD } 4.2$ ) and CRIII (mean  $16.2 \pm \text{SD } 3.6$ ) (ANOVA,  $F = 7.647$ ,  $\text{df} = 6$ ,  $P < 0.001$ , Tamhane post-hoc test,  $P < 0.001$  and  $P < 0.01$ , respectively). In all other forests, spider communities differed not significantly in respect to the proportion of singletons per community. Equitability, as measured by Simpson's index, was least in the disturbed forests and most in SII and SIII. Due to the numerical dominance of an individual species, unknown genus cf. *Pycnaxis* sp. (Thomisidae), which occurred on 13 out of 27 trees with maximum 71 and 86 individuals per tree, the primary forest evenness was lower. However, excluding this species from the analysis resulted in an index of 84.0, confirming high evenness for all other species.

Rarefaction curves did not level off with increasing size of sub-samples (Fig. 2). However, in contrast to the isolated forests, the curves were much steeper in the primary and the connected Sorinsim-forests indicating that spider communities were not collected representatively. Also Fig. 2 shows the clear separation between forest types, indicating that spider communities recovered much faster in the Sorinsim forests, which were adjacent to the primary forest, than in the isolated forests (see also Table 2). The increase of the rarefaction curve of SII indicates that the rate of species collection was similar to that of the primary forest. Prominent was the high species diversity of the 40 year-old forest SIII. Figure 3 shows the species frequency distribution of all spiders from all pooled foggings. Increasing the sample size always resulted in many new species indicating that the regional species pool was not sampled representatively by the 80 first foggings. Computing Shinozaki-curves for the four largest families, however, showed that they were collected reliably by fogging.

Comparing mean similarities of tree-specific spider communities (expressed by the Sørensen index, Fig. 4) showed clear differences between forest types (Mantel-test, Monte Carlo randomization,  $z = -0.583362$ ,  $P < 0.001$ ). In the primary forest and also in SI, SII, and SIII, 70% to 80% of all species were found only on one tree. In contrast, tree specific spider communities in the isolated forests shared many more species and consequently

communities showed a significantly higher overlap in species.

Most spiders were found only in one forest type: 155 species (52%) of primary forest species were restricted to the primary forest, 149 species (48%) and 62 species (38%) respectively were only found in the adjacent and the isolated forests. Changes in spider communities came along with drastic faunistic changes. For example, 96 widespread ubiquitous species (species distributed in the Malay Archipelago) were identified. Their proportion was highest in the isolated forests representing 56 of all 160 species (35%), 69 ubiquitous species (21.9%) were collected in the primary forest and 63 species (18.9%) in the connected 'Sorinsim' forests (Appendix 1). Most of the ubiquitous species were Araneidae, Theridiidae and Tetragnathidae and could be identified to the species level, like *Neoscona vigilans* (Blackwall 1865), *N. punctigera* (Doleschall 1857), common *Cyclosa* and *Gasteracantha* species, *Chrysso spiniventris* (O.P. Cambridge 1869), *Takayus lyricus* (Walckenaer 1842), *Tetragnatha hasselti* (Thorell 1890) and *Mesida gemmea* (van Hasselt 1882) (Platnick 2005; Yin et al. 1997; Zhu 1998; Zhu et al. 2003; Yoshida 2003).

## DISCUSSION

Anthropogenic destruction of tropical rain forests makes it necessary to assess the immediate and the long-term consequences for man and nature. Only on the basis of such knowledge is a sound nature protection plan possible. This, however, requires a high effort of basic research because even the extent of species richness is not known for most taxa (Basset et al. 2003). In this paper we present such a basic study for arboreal spiders, which we collected by pyrethrum knockdown fogging in primary and secondary lowland rain forests of Sabah, Malaysia on Borneo. Next to Formicidae, spiders are the most abundant group of predators in tropical lowland forest canopies (Adis et al. 1984; Stork 1991; Floren & Linsenmair 1997, 2001). Our study confirmed high species diversity of arboreal spiders. Despite a total of 102 foggings, the regional species pool was not sampled representatively and new species are still being found in new samples (Deeleman pers. obs.). There is a need to extend investigations, including further yet unsampled habitats, and

Table 2.—Comparison of spider communities between forest types. Analysis is based on first foggings only. Means are given with standard deviations. \* = Data are standardized for a crown projection of 1m<sup>2</sup> and a leaf cover of 100%. SI, SII, SIII = secondary forests connected with primary forests; CRI, CRII, CRIII = isolated secondary forests.

	Prim. forest	SI 5 yrs.	SII 15 yrs.	SIII 40 yrs.	CRI 10 yrs.	CRII 20 yrs.	CRIII 50 yrs.
Mean rel. prop. of spi- ders per for- est	5.6	7.2	4.6	5.9	9.8	6.3	6.4
No. of families	28	15	24	24	11	15	19
Rarefied no. of families (m = 306)	21.6	14.5	22.2	20.5	11	14.1	16.2
No. of species	296	120	127	230	65	97	102
Rarefied no. of species (m = 306)	122	94	115	132	65	77	77
William's al- pha	87.5	48.6	67.1	91.0	25.3	35.4	34.6
Total number of spiders collected	2488	525	365	1048	306	523	625
Standardized mean abun- dance*	19.6 ± 15.63	13.0 ± 7.8	6.4 ± 2.9	14.8 ± 5.3	15.8 ± 6.2	11.7 ± 8.1	11.6 ± 6.6
Singletons	96 (32.4%)	46 (38.3%)	61 (48.0%)	86 (37.4%)	27 (41.5%)	40 (41.2%)	35 (34.3%)
Mean propor- tion of sin- gletons of all trees	25.8 ± 11.8	17.4 ± 7.9	17.5 ± 6.3	33.8 ± 10.3	10.3 ± 4.2	17.6 ± 6.9	16.2 ± 3.6
Simpson-index	30.6	20.3	41.3	44.1	16.3	18.0	22.6

compare spider diversity with that reported in the few studies that have been carried out so far in the region (Russell-Smith and Stork 1994, 1995; Deeleman-Reinhold 2001) in order to assess the extent of diversity and to investigate the role spiders play in ecosystem functioning (New 1999).

Primary forests differ conspicuously from disturbed forests in habitat complexity. As a consequence, the diversity, structure, and dynamics of arthropod communities also change in disturbed forests (Floren et al. 2001). This was also confirmed, convincingly, for arboreal spiders. Using the primary forest as a basis, we investigated how spider communities changed in various secondary forests of different ages; that is to say in forests of different disturbance levels. Our data do not allow us to perform a full community level analysis because local species pools have not been sampled representatively and differences between

communities might simply be due to collecting new species. However, we can compare data after standardization, e.g. by using rarefaction statistics, comparing relative proportions of a parameter or by looking for changes in community structure and faunistic composition. On the basis of such comparisons, primary forests are clearly distinguishable from the adjacent secondary forests (SI, SII, SIII) merging into the primary forest, which are, themselves, clearly separated from the isolated forests (CRI, CRII, CRIII). As demonstrated by our data, the comparatively small distance of 10 km to the primary forest forms an effective barrier preventing species recolonization when the surroundings are cultivated land.

Spider density was similar in all forests indicating that the number of spiders collected by fogging did not depend on the tree species or the level of disturbance of the secondary



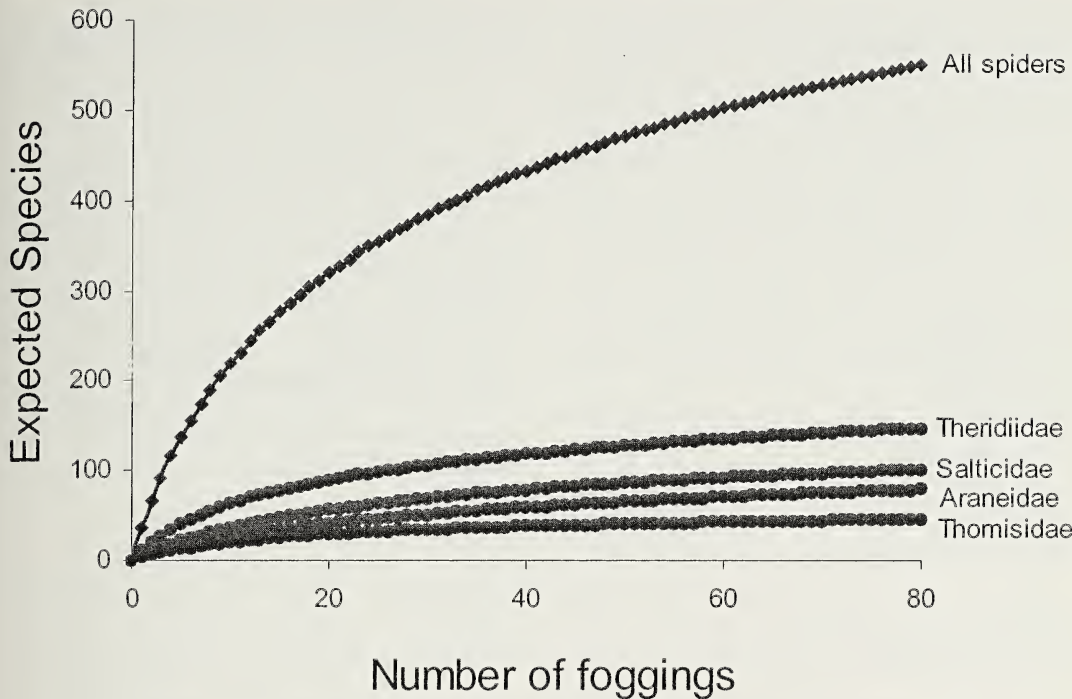


Figure 3.—Shinozaki curves of spider communities based on all foggings.

forest. Changes in spider communities occurred already at the family level (number of families collected per forest type) and were recognizable especially by the dominance of species from the families Theridiidae, Thomisidae, Salticidae, Araneidae, and Clubionidae. Dominance of individual species was highest in the most disturbed forests. Above all, high species diversity in SII and SIII indicate that the spider fauna recovered much faster in the forests close to the primary forest than in the isolated forests. An approximation to the conditions of the primary forest during the course of forest succession is obvious in most parameters analyzed and is in correspondence with similar findings for Formicidae and Coleoptera (Floren et al. 2001; Floren & Linsenmair 2001). In contrast, diversity in the isolated forests was significantly lower and changed only a little during forest regeneration. Species numbers give an impressive example: even in the 5 year-old pioneer forest SI, we found more species than in the 50 year-old isolated forest CRIII. Interestingly, the 40 year-old forest SIII was richer in species than the primary forest. A probable reason for this is that many primary forest species had already become established in SIII and were

able to coexist with species that were more successful under the disturbance regime. Although spider communities of the connected forests SII and SIII resembled those of the primary forest in many respects, there were still clear differences. While the proportion of singletons was larger than 30% in each forest type and did not correlate with the degree of disturbance, the mean number of singletons per tree community distinguished the primary and the old secondary forest SIII from all other disturbed forests. The number of singletons per tree-specific community was lowest in CRI, the youngest isolated and most disturbed forest fragment investigated. The low proportion of singletons per community corresponded with low overall diversity in the disturbed forest fragments and seems to be a good discriminator between primary, old-secondary and more severely disturbed forests. Community equitability also changed with forest disturbance from even communities in the primary forest to uneven communities in the disturbed forests. Similar changes are usually observed as a consequence of anthropogenic disturbance of forests (e.g., Leigh et al. 1993; Laurance 1994; Daily & Ehrlich 1995). The reason for the high abundance of

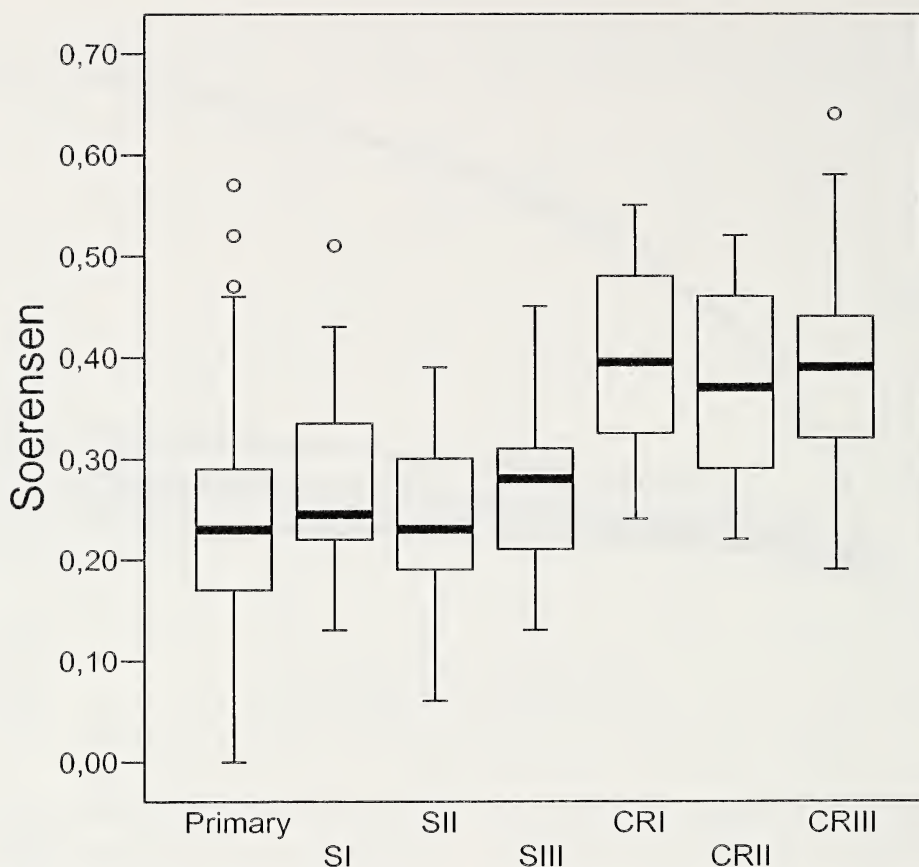


Figure 4.—Mean beta-diversities (measured by the Soerensen-index) between all spider communities of each forest type, expressed as Box Plots. The boxes cover 50 percent of all values (whiskers 75%) and show the median. A circle indicates outlier values between one and three times the box length.

the thomisid new genus & species cf. *Pycnaxis*, a species which seems unrelated to any other species and which has been found exclusively in the primary forests in Sabah, is not currently understood. It might be connected to the El Niño droughts of the year of collection in 1998. Spider communities became structurally simpler in the disturbed forests, because fewer species were found with median abundance classes. In the isolated forests we found a dominance of a number of common widespread web-building spider species: for instance several *Gasteracantha* and *Tetragnatha* species, *Mesida gemmea* (Hasselt 1882), and a number of smaller theridiid species. Several tiny (2–3 mm) widespread oonopid and theridiid species were found exclusively in the primary forests; these species probably live among the roots of epiphytic plants.

Our results led us to conclude that recolo-

nization from primary forests is absolutely necessary for the restoration of species diversity. If such species-sources are lacking, the restoration of spider diversity and spider communities proceeds only slowly if at all. These data indicate that the time necessary for recovery of arthropod diversity is usually greatly underestimated. The process of recolonization needs decades even under optimal conditions. In contrast, we sampled only rudimentary spider communities in the isolated secondary forest stands where no recolonization occurred. Even after 50 years of forest regeneration, spider communities were of low diversity and dominated by common species characteristic of open vegetation and shrub. Today small forest fragments dominate the landscape and already 40 year old forests are under high pressure by local people and the wood industry. Our study led us to suspect that the loss of spider species diversity will be



immense with primary forests lacking as species-sources from which recolonization can start.

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Appendix 1.—Number of species per family and number of widespread species in all fogging samples.

Sampling area	Primary forest		Secondary forests close to prim. forest		Secondary isolated forests		Total
	Ind.	Sp.	Ind.	Sp.	Ind.	Sp.	
No. of foggings	30		48		24		102
No. of families	26		23		20		29
Oonopidae	150	6	47	5	75	5	7
Pholcidae	147	10	3	2	7	2	11
Scytodidae	6	1	0	0	1	1	1
Clubionidae							
Clubioninae	230	17	54	15	21	4	24
Systariinae	18	3	0	0	0	0	3
Eutichurinae	14	2	12	2	5	1	4
Corinnidae							
Castianeirinae	40	9	64	7	10	3	10
Trachelinae	34	3	31	2	0	0	4
Phrurolithinae	2	1	17	1	2	1	3
Gnaphosidae	8	3	11	4	0	0	5
Sparassidae	71	6	59	7	42	3	10
Ctenidae	2	1	1	1	0	0	1
Selenopidae	3	1	0	0	0	0	1
Salticidae	334	59	426	65	72	19	111
Zodariidae	9	2	11	3	0	0	3
Oxyopidae	41	6	45	8	0	0	8
Pisauridae	0	0	21	1	1	1	1
Thomisidae	570	31	767	54	223	19	74
Philodromidae	15	2	5	2	12	1	2
Hahniidae	21	1	0	0	0	0	1
Hersiliidae	65	6	28	3	14	1	6
Linyphiidae	47	6	33	4	4	2	8
Theridiidae	562	80	600	83	631	53	153
Mimetidae	24	2	2	1	0	0	2
Theridiosomatidae	1	1	109	5	7	2	6
Tetragnathidae	98	10	117	10	171	9	19
Araneidae	151	36	307	44	97	29	80
Mysmenidae	0	0	10	6	2	1	7
Anapidae	0	0	5	2	1	1	3
Uloboridae	32	4	41	3	32	1	5
Dictynidae	43	1	0	0	0	0	1
Psechridae	2	2	0	0	1	1	2
Deinopidae	2	2	0	0	0	0	2
Total species		314		332		160	578
Identified widespread species		69		63		56	
Percentage widespread species		21.9%		18.9%		35.0%	

## GENDER SPECIFIC DIFFERENCES IN ACTIVITY AND HOME RANGE REFLECT MORPHOLOGICAL DIMORPHISM IN WOLF SPIDERS (ARANEAE, LYCOSIDAE)

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**ABSTRACT.** Sexual dimorphism of locomotory organs appears to be common in a variety of arthropods, however, the underlying evolutionary mechanisms remain poorly understood and may be the consequence of natural or sexual selection, or a combination of both. I analyzed the activity pattern of seven cohorts of a wolf spider, *Venatrix lapidosa*, over four consecutive years. Males appear to be the more active sex in search for a mate as they show temporarily higher activity prior to the periods of female brood care. Morphometric data on leg length showed comparatively longer legs for males than females. Allometric leg elongation in all four legs of males arises only after the final molt suggesting its significance in reproductive behavior such as mate search. A comparative analysis of two Australasian wolf spider genera with different activity profile of females, *Venatrix* (sedentary females) and *Artoria* (vagrant females) provides further evidence that limb elongation in males mainly arises due to indirect male mate competition.

**Keywords:** Sexual dimorphism, locomotion, leg length, mark and recapture, minimum convex polygon

Sexual dimorphism is thought to have evolved through sexual selection, ecological niche partitioning, differences in reproductive roles or a combination of these factors (e.g., Selander 1972; Hedrick & Temeles 1989; Shine 1989; Reynolds & Harvey 1994; Fairbairn 1997). Sexual selection arises through competition between members of one sex for reproduction with the other sex (Andersson 1994). Ecological niche partitioning may result in sexual dimorphism if each sex develops different structures as adaptations to different resources (Shine 1989; Walker & Rypstra 2001). Different reproductive success primarily arises through a fecundity advantage of large body size in females and is particularly evident in insects and spiders in which a common finding is that, throughout a wide range of sizes, female fecundity varies directly with mass (e.g., Head 1995; Prenter et al. 1999). Selection for early maturation of males (protandry) may also favor smaller male body size and thus result in sexual dimorphism (Bulmer 1983; Gunnarsson & Johnsson 1990). These explanations are not mutually exclusive and

thus sexual dimorphism could evolve in a species through both sexual and natural selection. Therefore, it is often difficult to determine what mix of influences has resulted in sexual dimorphism in a particular species (Hedrick & Temeles 1989).

The difficulty of identifying selective pressures is especially evident in the sexual dimorphism of locomotory structures, like wings or legs, which is a common phenomenon in many arthropods (Montgomery 1910; Thornhill & Alcock 1983). The evolution of gender specific differences in locomotory organs may be favored by both selection on male mate searching behavior and natural selection on female movements in relation to foraging or oviposition. Therefore, sexual dimorphism of locomotory structures has generally not been considered in studies of sexual selection (Darwin 1871; Andersson 1994). Gender specific differences in locomotory structures have usually been attributed to a more active behavior of one sex, typically males, in search for mates (Thornhill & Alcock 1983; Gasnier et al. 2002). Higher mobility may increase encounter rates of males with females and therefore increase fertilization success. However, gender specific elongation of limbs, even if under the influence of

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sexual selection, may not indicate an advantage in locomotion. Male elongated legs are important for direct male competition for mates in water striders (Tseng & Rowe 1999) and megalopodine beetles (Eberhard & Marin 1996), in grasping females during mating in mayflies or calanoid copepods (Peters & Campbell 1991; Ohtsuka & Huys 2001), in newt courtship displays (Malmgren & Thollesson 2001) and to reduce the risk of sexual cannibalism in some orb-web spiders (Elgar et al. 1990). In cursorial spiders, elongated segments of legs, in particular the first pair, have also been reported in combination with ornamentations in species with visual courtship display (Kronstedt 1990; Hebets & Uetz 2000). Therefore, it is vital to correlate activity and mobility patterns with sexual dimorphism of leg length to provide evidence of sexual selection acting on locomotion itself.

Sexual dimorphism in spiders has been studied extensively, however, the evolution of sexual size dimorphism remains controversial (e.g., Elgar 1991; Vollrath & Parker 1992; Head 1995; Hormiga et al. 1995). There are two main explanations for patterns of sexual size dimorphism in spiders (see Elgar 1998). Firstly, fecundity selection may favor larger females (Prenter et al. 1997, 1998, 1999). Alternatively, Vollrath & Parker (1992) suggest that sexual dimorphism may arise from differences in male and female lifestyles. In species with sedentary females, an increase in male mortality through mate searching behavior relaxes selection for large male body size and thus selection for protandry will favor smaller males. Ground living spiders are generally less size dimorphic than web-building species, which has been explained by their differing reproductive and foraging strategies (Enders 1976; Prenter et al. 1999). There is some evidence for sexual dimorphism in locomotory structures in ground living spiders (e.g., Gasnier et al. 2002). Montgomery (1910) reported that males have relatively longer legs than females, which he suggested is a result of the nomadic behavior of males after attaining sexual maturity. This idea is supported by a number of short term studies on the locomotory activity of wolf spiders, in which males were the more active sex (e.g., Hallander 1967; Richter et al. 1971; Cady 1984; Framenau et al. 1996a). However, wolf spiders differ in activity profiles due to vary-

ing life strategies that range from permanently burrowing (e.g., *Geolycosa* or *Lycosa* s. str.), to permanently vagrant animals (e.g., *Pardosa* and *Pirata*; e.g., Dondale & Redner 1990). These different lifestyles are reflected in mechanics of locomotion and activity response to variation in food supply (Ward & Humphries 1981; Walker & Rypstra 2001). Therefore, it is important to analyze sexual dimorphism in locomotory organs in conjunction with data on the general activity pattern over an adult spider's life span.

The goal of this study was to relate the activity profile of males and females of a cursorial wolf spider, *Venatrix lapidosa* (McKay 1974), to gender specific differences in the morphology of their locomotory organs. The activity profile of these spiders was generated by conducting a fortnightly mark and recapture survey over a period of more than three years, covering seven generations of adult spiders. This allowed an analysis of both the variation of spider activity over their entire adult life, and incorporated seasonal variation, thus contrasting with all previous studies of wolf spiders that typically observed individuals for only up to a day (Richter et al. 1971; Cady 1984). I was not only interested in each individual's activity (i.e. movement per unit time), but also the spatial aspect of movement (home range). Increases of both variables have the potential to augment fertilization success of males by increasing their encounter rates with females. However, these variables may not co-vary and higher activity may not necessarily increase home range size. Differential spatial use by males and females, as inferred from their home range, may also influence the operational sex ratio, thereby affecting the potential for male-male competition. Lastly, I analyzed locomotory structures of two Australasian genera of wolf spiders, *Venatrix* and *Artoria*, with different activity profiles of females to determine if differences in behavior are reflected in leg length dimorphism across a higher taxonomic level.

## METHODS

**Study species.**—*Venatrix lapidosa* is a nocturnal wolf spider inhabiting riparian gravel banks in southeastern Australia (McKay 1974; Framenau & Vink 2001). It is a vagrant species, but brood caring females, and all spiders during overwintering, dig excavations

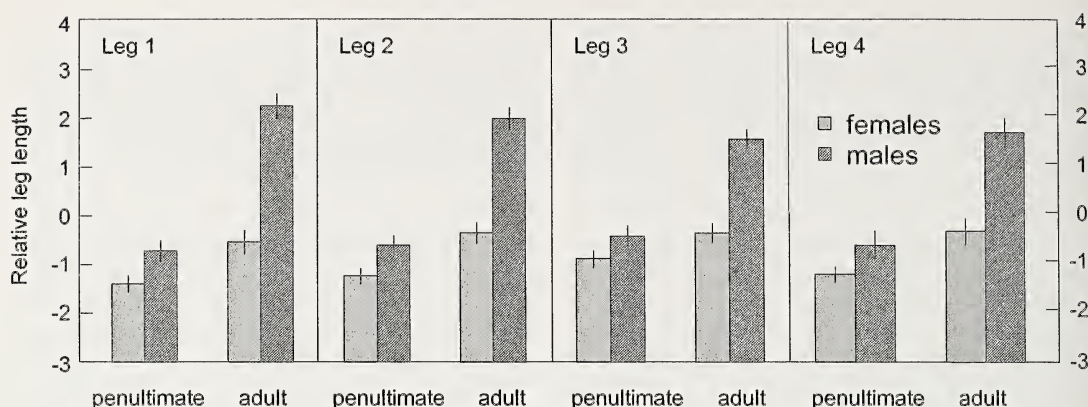


Figure 1.—Relative leg length (residuals of leg length on cephalothorax width) (mean  $\pm$  s.e.) of female and male penultimate and adult *Venatrix lapidosa*. For statistical analysis (ANOVA) see Table 1.

under rocks that they line with a thin layer of silk (Framenau 1998, 2002a). *Venatrix lapidosa* is biennial, with juvenile development requiring up to 16 months. Adult life span of females may be up to eleven months and that of males up to ten months (this study; also Framenau & Elgar 2005). However, the average life span of adults of both sexes does not generally exceed 6 months. The life cycle of *V. lapidosa* in the Victorian Alps is characterized by the maturation of two distinct cohorts within each year (Framenau & Elgar 2005). In autumn maturing cohorts, most individuals mature between March and May, enter winter diapause, reproduce only after overwintering and die by December. In spring maturing cohorts, spiders molt to maturity between November and January, reproduce immediately and most spiders die by May. Overlap between adult individuals of both cohorts is minimal and generally limited to a low number of long-lived individuals that reach the maturation period of the following cohort. Laboratory-reared males and females of different cohorts readily mate (Cutler 2002) and this overlap permits gene flow between the different cohorts. Winter covers a large period of the adult life span of autumn maturing spiders, whereas adult individuals of the spring maturing cohorts live over summer, so cohorts were expected to differ considerably in their activity profile.

**Morphology of *V. lapidosa*.**—I collected adult (9 females, 15 males) and penultimate (15 females, 12 males) *V. lapidosa* from a variety of populations at ten rivers in seven ma-

jor catchments during a survey of riparian gravel banks in the Victorian Alps between November 1999 and January 2000 (Framenau et al. 2002). Leg length (sum of all segments measured dorsally) of all four pairs of legs was determined under a stereomicroscope to the nearest 0.1 mm. Carapace width was measured above the coxae of the second pair of legs as an indicator of spider size (Hagstrum 1971; Jakob et al. 1996). I included penultimate spiders in the analysis to establish if an allometric increase in leg length occurs during the last molt, potentially indicating the importance of dimorphism for mature, sexually active spiders. Younger than penultimate spiders were not used as it was impossible to establish their sex. Gender specific differences in leg length were analyzed using the residuals of a least squares regression using leg length on cephalothorax width over both sexes and adult and penultimate spiders. This gives rise to measures of relative leg length, which were independent of body size. Residuals between the sexes and adult and penultimate spiders were compared by two-way ANOVA.

**Mark and Recapture.**—The mark and recapture study of *V. lapidosa* was conducted on a gravel bank at the Avon River near Valencia Creek in Victoria, southeastern Australia (37°48'S, 146°27'E). The climate of the region is moderate with mean daily maximum and minimum temperatures of 20.0 °C and 8.0 °C, respectively. Annual rainfall averages 594 mm (Data from Maffra Forestry Office; Bureau of Meteorology, Melbourne). The gravel bank studied was bordered by the Avon River



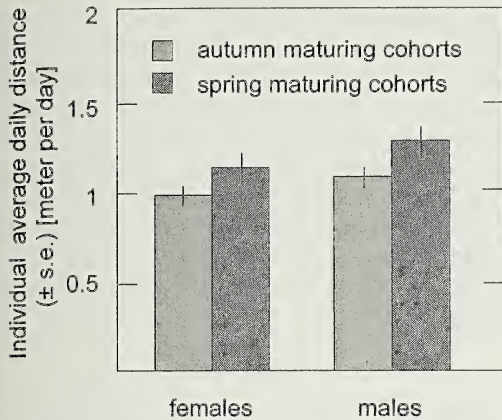


Figure 2.—Individual average daily distances (meters per day; mean  $\pm$  s.e.) of female and male *Venatrix lapidosa* from the autumn and spring maturing cohorts at the Avon River. Average daily distance moved based on two-week interfix intervals. To determine individual average daily distances, all average daily distances measured during the life span of one individual were averaged.

on the southern side and a dense cover of vegetation (wattle, *Acacia trilobata*, willow, *Salix* sp. and blackberry, *Bromus* sp.) on a steep slope on the northern side, keeping spider immigration and emigration minimal. With the exception of a few *Acacia* and *Salix* shrubs, the gravel bank was bare of vegetation. When the survey commenced in 1996, the surface area of the bank was 1,830 m<sup>2</sup>. In August 1998, it diminished in size to 1,540 m<sup>2</sup> due to a severe flood.

A 5 m  $\times$  5 m grid was established on the gravel bank using wooden pegs. One co-ordinate of this grid ('Y'-value) was perpendicular to the river and therefore expressed the relative distance from the water. Surveys were conducted fortnightly, from 8 November 1996 to 2 May 2000. This observation period covered four spring maturing cohorts (1996–1999) and three autumn maturing cohorts (1997–1999) (Table 2). All rocks large enough to provide shelter for spiders were overturned and replaced. Each survey started randomly at either end of the gravel bank. Each grid was examined in a spiral from exterior to interior, in order to prevent spiders from leaving a grid while it was searched. Spider locations were determined to within an accuracy of 1 m. New adult spiders in the population were individually marked with a bee tag glued to their cephalothorax using a cyane-acrylate based

adhesive (Supaglu Gel<sup>TM</sup>). Cephalothorax width and body length were determined with vernier callipers to the nearest 0.1 mm. When returned, most spiders either remained without any movement under the same rock, or found shelter under the next available rock. Initial disturbance was therefore considered minimal. On subsequent encounters, only a spider's position was recorded to avoid further disturbance.

Activity was determined using the average daily distance ('velocity' in Samietz & Berger 1997), which is defined as the distance between two consecutive fixes divided by the days between both observations. Not all spiders were recaptured every survey and average daily distances significantly decreased with the time lapsed between two consecutive fixes (two-, four-, six-, eight-weekly interfix intervals;  $R^2 = 0.072$ ,  $P < 0.001$ ,  $n = 2,706$ ). Thus, only average daily distances based on recaptures within two weeks of a previous one were considered in the analysis. In addition, these shorter intervals provided the most accurate picture of a spider's movement. I compared individual activity of males and females ('individual average daily distance') and autumn and spring maturing cohorts by their mean average daily distances over the whole observation period. To analyze seasonal variability of activity, average daily distances were also determined for each month of the year pooled over all individuals of each sex but analyzed separately for autumn and spring maturing cohorts. In this case, the average daily distance was obtained by analyzing captures within two consecutive months were assigned to the month that contained most days of the interfix interval. I pooled monthly data over all years after establishing that there was no between year variation.

**Home range.**—I estimated home ranges using 100% minimum convex polygons (MCP; Mohr 1947). For low capture numbers, MCPs increase with each additional fix until a stable home range is reached. Regression analysis identified nine as the minimum number of captures from which an increase in fixes did not result in a further, significant increase in home range size ( $R^2 = 0.008$ ,  $P = 0.397$ ,  $n = 91$ ). Increment analysis of home ranges (Kenward & Hodder 1996) showed that nine fixes provided an average of 90% of the full home range. This conforms to results of Sam-

ietz & Berger (1997), who show that home ranges (100% MCP) for insects appear to be stable from 10 captures. Two-week observation periods guaranteed temporal independence of subsequent fixes, which is assumed if an animal can cross its home range within this period (White & Garrott 1990). As a measurement of home range shape, I calculated the range span as the distance of the furthest two points in a home range. Range centers were calculated as the mean of the X- and Y-values, corresponding to the established grid, of all fixes in a home range. Only one range in the spring maturing cohorts was based on more than eight fixes (Table 2). Therefore, between cohort analysis of home range size and range span was not possible.

Home range overlap was calculated for pairs of spiders that belonged to the same cohort and so could potentially meet. Two values of home range overlap could be determined for each pair of spiders, i.e. how much of the home range of spider A was overlapped by the range of spider B, and vice versa. I used the average of both values as the measurement of range overlap.

**Comparative morphology.**—The taxonomy of only two Australasian wolf spider genera, *Venatrix* Roewer (Framenau & Vink 2001; 23 species) and *Artoria* Thorell (Framenau 2002b; 11 species) is known sufficiently to allow interspecific comparative analyses. Both genera differ considerably in their mobility pattern, as most females of *Venatrix* dig permanent burrows or construct temporary excavations during brood care, whereas females of *Artoria* are vagrant throughout their life (Framenau 2002b; also pers. obs). Least squares regression of leg length on cephalothorax width for all pairs of legs over all species derived from the primary taxonomic literature of both genera (Framenau & Vink 2001; Framenau 2002b) provided measures of relative leg length (residuals) compared to a 'typical' lycosid. To test for sexual dimorphism within both genera, these residuals were compared between the sexes using two-sample t-tests.

**Statistical analysis.**—Home range and activity parameters were calculated using the software package 'RANGES V' (Kenward & Hodder 1996). Subsequent statistical analyses were performed with 'SYSTAT Version 9' (SPSS Corp. 1998). Data that did not comply

with ANOVA assumptions were log-transformed, in case of average daily distances (log + 1)-transformed (Quinn & Keough 2002). If normality of data could not be achieved, non-parametric tests (Mann-Whitney U Test) were used to compare sexes. Measurements are given as mean  $\pm$  standard error (s.e.) unless otherwise indicated. Voucher specimens of *V. lapidosa* were deposited at the Museum Victoria, Melbourne, and the Western Australian Museum, Perth.

## RESULTS

**Morphology of *V. lapidosa*.**—The carapace width ( $\pm$  s.e.) of adult female *V. lapidosa* ( $6.66 \pm 0.18$  mm,  $n = 9$ ) was significantly larger than that of males ( $5.91 \pm 0.06$  mm,  $n = 15$ ; separate  $t = 4.019$ , d.f. = 10.2,  $P = 0.002$ ). The length of all legs was positively correlated with cephalothorax width and residuals of these regressions yielded measures of relative leg length (Table 1). All legs were comparatively longer in males than in females for adult and penultimate spiders (Table 1, Fig. 1). A significant interaction between age and sex for all legs indicates a proportionally higher elongation (allometric growth) for male legs during their last molt compared with females (Fig. 1).

**Mark and recapture survey.**—A total of 741 males and 712 females were individually marked over a period of 3.5 years, yielding an overall even sex ratio ( $\chi^2 = 0.802$ ,  $P = 0.37$ ) (Table 2). However, recapture rates, i.e. how often individual spiders were caught, differed significantly for males and females (Mann-Whitney  $U = 314226.5$ ,  $P = 0.008$ ) due to a higher number of males encountered only once. The total number of fixes analyzed was 4,963 yielding a detailed life cycle profile for each cohort in each year (see Framenau & Elgar 2005).

**Activity.**—Mean average daily distances of individual spiders, based on two-week interfix intervals, were significantly higher for males than females, and higher for individuals of the spring mating cohorts than of the autumn maturing cohorts (two-way ANOVA; sex:  $F_{1,699} = 6.045$ ,  $P = 0.014$ ; cohort:  $F_{1,699} = 4.816$ ,  $P = 0.029$ ; interaction:  $F_{1,699} = 0.384$ ,  $P = 0.536$ ) (Fig. 2).

Monthly average daily distances in the autumn cohort showed no significant difference between sexes (two-way ANOVA;  $F_{1,1186} =$



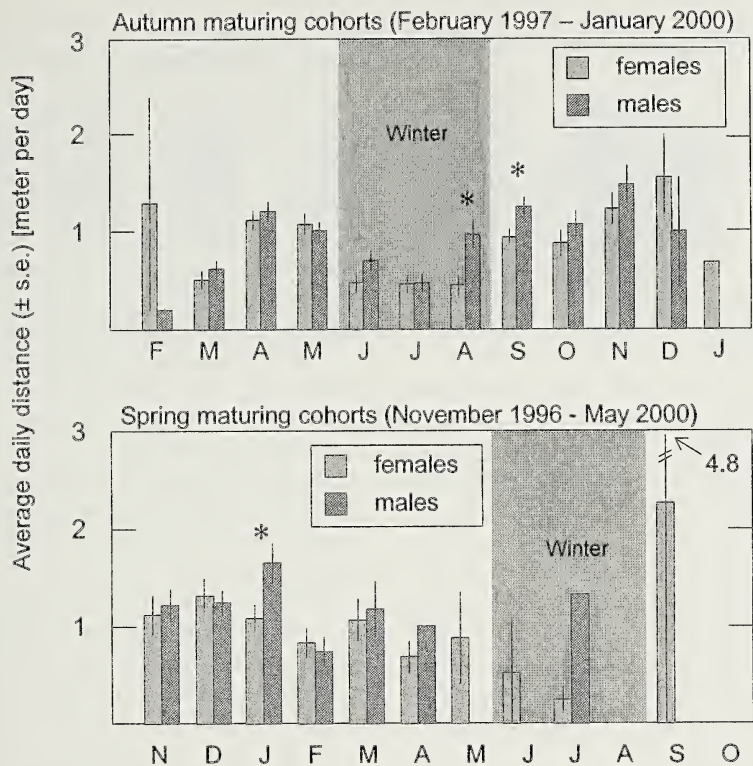


Figure 3.—Monthly average daily distances (meters per day; mean  $\pm$  s.e.) of female and male *Venatrix lapidosa* from the autumn and spring maturing cohorts during the survey at the Avon River. The month on the far left in each graph represents the maturation of each cohort. Average daily distance moved is based on two-week interfix intervals. To determine monthly average daily distances, all average daily distances within a month were averaged over all individuals. Asterisk (\*) indicates significant difference between sexes.

0.087,  $P = 0.769$ ), however, there were significant differences between months ( $F_{10,1186} = 7.908$ ,  $P < 0.001$ ; interaction:  $F_{10,1186} = 1.055$ ,  $P = 0.394$ ; January excluded due to missing variation between sexes; Fig. 3). In the spring cohort, there was also no overall gender specific difference in monthly average daily distances (two-way ANOVA;  $F_{1,389} = 1.514$ ,  $P = 0.219$ ) and, in contrast to the autumn cohort,

there was no differences between months ( $F_{5,389} = 2.188$ ,  $P = 0.055$ ; interaction:  $F_{5,389} = 0.892$ ,  $P = 0.486$ ; May–October excluded due to missing variance in sex or months; Fig. 3). However, a within months comparison of average daily distances between males and females revealed significantly higher male activity in August (pooled  $t = 3.048$ , d.f. = 28,  $P = 0.005$ ) and September (pooled  $t = 2.199$ ,

Table 1.—Comparison of relative leg length (residuals of leg length on carapace width) between male and female and adult and penultimate *Venatrix lapidosa*. Regression of leg length on carapace width: Leg 1:  $R^2 = 0.543$ , slope = 2.978,  $P < 0.001$ ,  $n = 51$ ; leg 2:  $R^2 = 0.608$ , slope = 2.972,  $P < 0.001$ ,  $n = 51$ ; leg 3:  $R^2 = 0.689$ , slope = 2.909,  $P < 0.001$ ,  $n = 51$ ; leg 4:  $R^2 = 0.672$ , slope = 3.457,  $P < 0.001$ ,  $n = 51$ . Given are the  $F_{1,47}$ -values and significance level (\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ ) of a two-way ANOVA.

Factor	Leg 1	Leg 2	Leg 3	Leg 4
Sex	60.918***	55.644***	35.171***	26.328***
Age	74.322***	76.209***	39.534***	39.378***
Interaction: Sex * Age	22.746***	18.380***	13.416**	7.923**

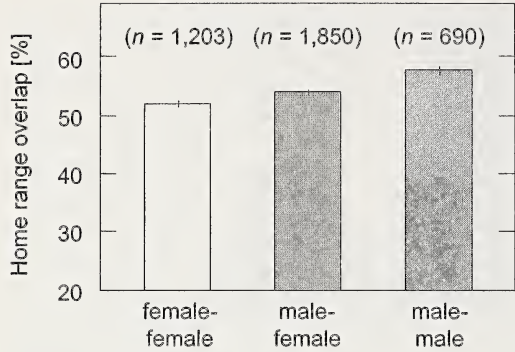


Figure 4.—Intra- and intersexual home range overlap (mean  $\pm$  s.e.) in *Venatrix lapidosa* within the 1997 autumn maturing cohort. No other cohort provided a sufficient number of home range estimates to compare between and within sexes (see Table 1).

d.f. = 221,  $P = 0.029$ ) for the autumn cohort and in January (pooled  $t = 2.673$ , d.f. = 120,  $P = 0.026$ ) for the spring cohort (Fig. 3).

**Home range.**—Due to the major flood in 1998, home range overlap analysis was restricted to the autumn 1997 cohort when males and females were caught in sufficient numbers (minimum of nine fixes) to allow a comparison between the sexes (Table 2). Therefore, a comparison between cohorts was not possible. Home range estimates (100% MCP  $\pm$  s.e.) did not differ significantly between males ( $302 \pm 16 \text{ m}^2$ ,  $n = 42$ ) and females ( $311 \pm 17 \text{ m}^2$ ,  $n = 49$ ; pooled  $t = 0.375$ , d.f. = 89;  $P = 0.709$ ). Home range span also did not differ between males ( $55.4 \pm 2.1 \text{ m}$ ,  $n = 42$ ) and females ( $53.7 \pm 2.2 \text{ m}$ ,

$n = 50$ ; pooled  $t = 0.548$ , d.f. = 89;  $P = 0.585$ ). Home range centers did not show a significant difference between sexes along the river (X-coordinate; pooled  $t = 1.732$ , d.f. = 89;  $P = 0.087$ ), but the relative distance from the river (Y-value) was significantly higher for females ( $10.1 \pm 0.2$ ,  $n = 49$ ) than males ( $9.3 \pm 0.2$ ,  $n = 42$ ; pooled  $t = 3.156$ , d.f. = 89;  $P = 0.002$ ). In addition, females carrying an eggsac were found significantly further away from the water (Y-coordinate  $\pm$  s.e.;  $9.8 \pm 3.3$ ,  $n = 124$ ) than females not caring for brood ( $9.0 \pm 3.0$ ,  $n = 1,179$ ; pooled  $t = 2.372$ , d.f. = 1301;  $P = 0.018$ ). Overall, range overlap was high ( $> 50\%$ , Fig. 4), but it differed significantly between sexes, with male-male overlap highest and female-female overlap lowest (ANOVA;  $F_{2,3743} = 19.315$ ,  $P < 0.001$ ) (Fig. 4).

**Comparative morphology.**—There was a positive correlation between cephalothorax width and leg length in both *Venatrix* and *Artoria* and measures of relative leg length were obtained from the residuals of the respective regressions (Table 3, Fig. 5). Males had comparatively longer legs than females within the genus *Venatrix*, but there was no gender specific difference in the relative leg length in *Artoria* (Table 3, Fig. 5).

DISCUSSION

There was a considerable difference in the activity and mobility pattern of male and female *V. lapidosa*, which corresponded to a pronounced sexual dimorphism in the length of their legs. The evolution of longer legs in

Table 2.—Capture statistics of the mark and recapture survey of *Venatrix lapidosa* at the Avon River, distinguished by cohorts. Average daily distance based on two-weekly interfix intervals only (see text). §Considered in analysis of average daily distances; ‡Considered in home range analysis.

	Cohort						
	Spring 1996	Autumn 1997	Spring 1997	Autumn 1998	Spring 1998	Autumn 1999	Spring 1999
Males:							
Total number marked	115	179	80	168	86	84	29
Recaptured at least once§	58	157	35	121	43	67	9
Minimum of nine captures‡	0	38	0	2	0	2	0
Females:							
Total number marked	127	176	105	140	77	66	21
Recaptured at least once§	88	158	72	96	48	56	7
Minimum of nine captures‡	1	48	0	0	0	0	0



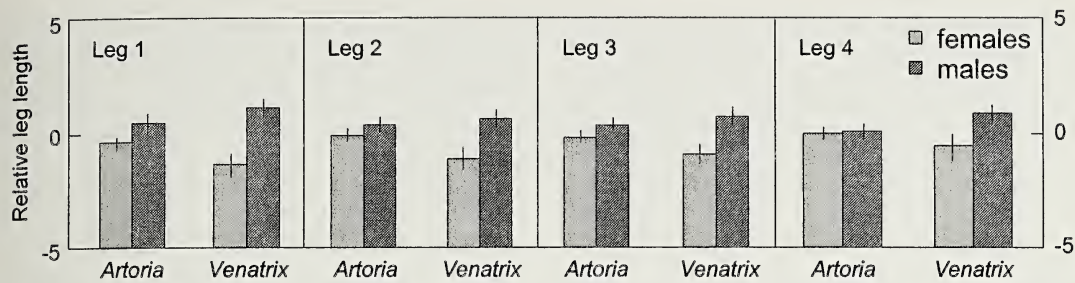


Figure 5.—Relative leg length (residuals of leg length on cephalothorax width) (mean  $\pm$  s.e.) of female and male species of *Venatrix* and *Artoria*. For statistical analysis between sexes in each genus (t-test) see Table 3.

males may be the result of an increased likelihood to encounter more stationary females assuming a higher energy efficiency or speed as a result of leg elongation. The lack of sexual dimorphism in leg length in juvenile *V. lapidosa* and the genus *Artoria* (in which females are vagrant) supports this argument.

**Activity.**—*Venatrix lapidosa* is a comparatively immobile spider. Similar low activity occurs in other cursorial spiders inhabiting terrestrial-aquatic ecotones (Framenau et al. 1996a; Kreiter & Wise 2001). Limited mobility of riparian species may be a result of their fragmented habitat consisting of generally small isolated gravel banks. In addition, high prey availability near the water edge may render it unnecessary to move (Greenstone 1983). As expected for poikilothermic animals, activity between cohorts differed, most likely reflecting seasonal patterns. Activity was lower for individuals of the autumn mating cohort, due to a drop in movement over winter. Individuals of the spring mating cohorts, although more active than the autumn mating cohorts, showed no significant difference in activity between months. These individuals are adults mainly in summer. Temperature dependent movement patterns have also been reported in other wolf spiders, such as *Pardosa amentata* (Clerck 1757) (Ford 1978).

Activity patterns of males and females are similar within both cohorts, with males the more active sex. A variety of studies on wolf spiders have shown that an increase in male activity reflects mate searching (e.g., Hallander 1967; Framenau et al. 1996a). In *V. lapidosa*, significantly higher male activity appears to be temporary, emerging about three months after maturation (delayed in the autumn maturing cohort by winter diapause). In

the autumn maturing cohort, males emerge earlier from diapause and are more active than females two months prior to female egg production, suggesting that males are searching for mates. Higher male activity in the spring mating cohort cannot be as easily explained in terms of mate searching, as male activity was particularly high in January, when females had already commenced egg production. Since higher male activity is observed for only a few months, females appear to move more than suggested by previous studies on wolf spiders (Richter et al. 1971; Hallander 1967). Initial female activity may be high due to increased foraging effort to meet energetic requirements for egg production (Kreiter & Wise 2001). Movement in female *V. lapidosa* may also be induced by the apparent preference of females to oviposit some distance from the water. Activity may subsequently drop, as females become sedentary to care for their brood (Hackman 1957; Hallander 1967; Framenau et al. 1996a, b; Nyffeler 2000). An unusually low proportion of ovipositing females in *V. lapidosa* (Framenau & Elgar 2005) compared to other lycosids (e.g., Framenau 1996a; Humphreys 1976) suggests a comparatively low number of stationary, broodcaring females and may partly explain why differences in activity between males and females is limited.

**Home range.**—Despite the temporary increase in male activity, home range size did not differ between males and females in *V. lapidosa*. The movements of *V. lapidosa* may have been restricted by the size of the study site itself, but average home range size and range span for both sexes were considerably smaller than the surface and length of the investigated gravel bank.

Table 3.—Comparison of relative leg length (residuals of leg length on carapace width) between males and females in species of the genera *Venatrix* and *Artoria*. Regression of leg length on carapace width: Leg 1:  $R^2 = 0.899$ , slope = 3.292,  $P < 0.001$ ,  $n = 51$ ; leg 2:  $R^2 = 0.912$ , slope = 3.037,  $P < 0.001$ ,  $n = 58$ ; leg 3:  $R^2 = 0.903$ , slope = 2.772,  $P < 0.001$ ,  $n = 58$ ; leg 4:  $R^2 = 0.892$ , slope = 3.512,  $P < 0.001$ ,  $n = 56$ . Given are the  $t$ -values (pooled variance) with significance level (n.s. non significant;  $*P < 0.05$ ,  $**P < 0.01$ ,  $***P < 0.001$ ) and degrees of freedom (d.f.).

Factor	Leg 1	Leg 2	Leg 3	Leg 4
<i>Venatrix</i>				
Sex	4.140***	3.056**	3.182**	2.039*
d.f.	33	34	34	34
<i>Artoria</i>				
Sex	1.832 n.s.	1.529 n.s.	1.642 n.s.	0.770 n.s.
d.f.	19	20	20	18

Although home range size was similar between the sexes, there was a significant difference in the distribution of range centers between females and males. Female range centers were, on average, located further away from the water as ovipositing females retreat from the border of the gravel bank. Females may not tolerate a high degree of soil moisture, or they may look for more protected areas from varying water levels, before excavation of brood chambers. Site specificity in relation to abiotic factors occurs frequently in lycosids that build permanent burrows (e.g., Humphreys 1976; Milasowszky & Zulka 1998). Females of *A. cinerea* (Fabricius 1777) and *Trochosa ruricola* (DeGeer 1778), two lycosids inhabiting shore habitats, also move away from the water prior to brood care (Hackman 1957; Framenau et al. 1996b). Differential microhabitat preferences can have a strong influence on the activity and distribution patterns of individuals. In wolf spiders, intraspecific habitat preferences not only differ between females with and without eggsacs (Edgar 1971; Hallander 1967; Greenstone 1983), but also between sexes (Cady 1984) and adults and juveniles (Edgar 1969, 1971; Kronk & Riechert 1979).

The utilization of areas further away from the water, together with equal home range size, may explain the lower female-female range overlap compared to males. In wolf spiders, males and females do not encounter each other haphazardly. Males follow silk draglines laid by receptive females which contain sex-attracting pheromones (Hedgekar & Dondale 1969; Tietjen & Rovner 1982). In addition, strong agonistic behavior within sexes has

been reported in wolf spiders (Aspey 1977a, b; Fernández-Montraveta & Ortega 1991). The effect of different habitat requirements, i.e. the search of a favorable location for brood care, appears to be stronger than male-female attraction or intrasexual aggression.

**Sexual dimorphism.**—*Venatrix lapidosa* is sexually dimorphic. Females are generally larger than males, but males have comparatively longer legs. The sex ratio of *V. lapidosa* was not biased in the autumn mating cohort, and limited to later months in the spring cohorts when many females were already caring for their brood (Framenau & Elgar 2005). Further, higher home range overlap between males suggests greater rather than less opportunity for male-male competition. Therefore, my data are not consistent with the underlying assumptions of the model developed by Vollrath & Parker (1992) that relates sexual size dimorphism in spiders to reduced male-male competition due to an increase in mortality caused by mate search. Sexual dimorphism in *V. lapidosa* most likely evolved through a fecundity advantage for larger females (Prenter et al. 1997, 1998, 1999); clutch size increases with body size in many wolf spider species (Marshall & Gittleman 1994; Simpson 1995).

While increased female fecundity may explain size differences between males and females, sexual selection through indirect male-male competition may explain the comparatively longer legs of males. Allometric growth leading to relatively longer legs only takes place in males and mainly during the final molt supporting an evolutionary hypothesis of leg elongation in males rather than leg shorting in females due to burrowing be-



havior. The production of longer legs may be ontogenetically costly and thus would be offset by energetically more efficient movement.

There are no experimental or comparative data of increased movement efficiency with longer legs in arthropods (J. Shultz pers. Comm.) and the relationship between leg dimensions (length and thickness) and metabolic rate are complex and also entail the mass of the spider. Simple lever mechanics predicts that if the length of the output lever arm increases, the velocity and excursion at the end of the lever will increase (and thus speed and distance moved per stride), but that the force the lever will exert will decrease (Manton 1977; Alexander 1982; Hildebrand & Goslow 2003). Males can compensate the loss of force by reducing their own mass which, in turn, augments selection for smaller males, providing a novel aspect in the explanation for sexual size dimorphism in vagrant spiders. Overall, longer-legged, smaller males are able to search faster and more extensively for females and potentially increase their encounter rates with females. This advantage would be favored by sexual selection if it provided males with a competitive edge in terms of fertilization success.

A limb elongation due to more efficient locomotion is also supported by the fact that all four legs show the same allometric pattern which was not required if the difference in leg length between sexes arose through sexual cannibalism (Elgar et al. 1990), male-male combats (Tseng & Rowe 1999), or in combination with leg ornamentation in used in courtship display (Kronestedt 1990; Hebets & Uetz 2000). In addition, sexual cannibalism and male-male combats are extremely rare in wolf spiders (Aspey 1977a). Alternatively, different foraging behavior between males and females could provide an explanation of sexual dimorphism based on different locomotory patterns (Givens 1978). However, due to lower metabolic requirements male wolf spiders attack considerably fewer prey than females (Walker & Rypstra 2001). Longer legs may also provide a sensory advantage due to an increased radius to mount olfactory chemoreceptors or trichobothria. In wolf spiders, olfaction plays some role in mate search, however, the main senses used by males to follow trail lines of females are situated on the dorsal

side of the cymbium of the pedipalps (Tietjen & Rovner 1982).

The comparison in the pattern of leg-length dimorphism in *Venatrix* and *Artoria* provide further evidence that male mate-searching behavior favors relatively longer legs in males. Although males in *Artoria* also tend to have longer legs than females, this difference is not significant within the genus and is far less pronounced than in *Venatrix*. It appears unlikely that leg length dimorphism arises through shortening of female legs due to burrowing behavior, as allometric growth occurs between penultimate and adult spiders. In addition, there is no evidence that female *Venatrix* have comparatively shorter legs than vagrant *Artoria*.

This study provides evidence that longer legs in male wolf spiders are mainly caused by sexual selection through indirect competition with increased male activity in searching for a mate. To further elucidate the selective forces responsible for the elongation of male legs, future work should focus on three questions. Firstly, it is important to experimentally confirm the assumption that longer legs are more energy efficient in spider movement. Secondly, evidence that higher male activity will ultimately lead to higher fertilization success is required. This is strongly dependent on the species mating system in question, and requires an understanding of multiple mating and sperm priority patterns of wolf spiders (Austad 1984; Elgar 1998). Although *V. lapidosa* has been reported to mate multiply increasing the chance of male mate competition (Cutler 2002), there is no information on sperm priority patterns in this and other Lycosidae. Lastly, comparative studies in leg length dimorphism in comparison with the life time activity patterns of cursorial spiders on a broader taxonomic base may help us understand to what extent sexual dimorphism of limbs are under natural or sexual selection.

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## EVOLUTION OF ORNAMENTATION AND COURTSHIP BEHAVIOR IN *SCHIZOCOSA*: INSIGHTS FROM A PHYLOGENY BASED ON MORPHOLOGY (ARANEAE, LYCOSIDAE)

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**ABSTRACT.** A phylogenetic analysis for the North American *Schizocosa* species was undertaken by scoring 49 morphological characters for 31 taxa representing all of the Nearctic species of *Schizocosa* plus individuals that are hybrids between *S. ocreata* and *S. rovneri*. *Rabidosa rabida*, *Allocosa georgicola* and *Gladicosa pulchra* were used as outgroups. Three clades are recognized: a large clade from eastern North America (Clade A) within which is nested the *S. ocreata* clade; Clade B, which includes the widespread *S. avida* and the western *S. mccooki*, and a smaller, third clade, Clade C. Sexual ornamentation occurs on the first legs of mature males of several species within the *Schizocosa* and takes the form of pigmentation and or bristles primarily on the tibia of leg I; there is at least one species with bristles in each of the three main clades. Mapping the occurrence of male ornamentation on the preferred phylogeny suggests that ornamentation evolved 5 or 6 separate times and was subsequently lost 2 or 3 times. The ornamentation is concentrated in the *S. ocreata* clade, a clade defined by a finger like projection on the paleal process of the male pedipalp. Courtship behavior is known for 20 of the 31 taxa. All species studied utilize chemical communication and seismic signals for communication; some species also have distinct visual signals. Seismic signals are produced by palpal drumming (as is seen in several species within Clade B), or by stridulation (seen in Clade A). Visual signals consisting of movements of the first pair of legs are common in species that are distinctly ornamented. This study provides the first phylogenetic study of a North American genus of wolf spider and provides morphometric comparisons of the North American species in *Schizocosa*.

**Keywords:** Cladistics, sexual selection, secondary sexual characteristics, evolution of behavior, spiders, multimodal signal, seismic signal

In spiders, sexual ornamentation is most evident in groups that have exceptional eyesight (e.g., Salticidae and Lycosidae) with ornaments being found on mature males in places that are visible to females or other males. In contrast to the colorful salticids (e.g. the North American genus *Habronattus* F.O.P Cambridge 1901, Peckham & Peckham 1889, 1890; Griswold 1987; Maddison & Hedin 2003), the ornamentation on lycosids tends to be in black or white, and is generally limited to the first pair of legs or to the pedipalps of mature males. Examples of such ornaments in wolf spiders are wide spread and include dark pigmentation on some part of the first pair of legs as seen in *Alopecosa aculeata* (Clerck 1757) and *A. barbipes* (Sundevall 1833) (Kronstedt 1990) or on the pedipalps as seen in *Pardosa wagleri* (Hahn 1822) and *P. saturatior* Simon 1937 (Barthel & Helvesen 1990) or *P. saxatilis* (Hentz 1844) (Dondale & Red-

ner 1984). In addition, many members of the North American *Geolycosa* Montgomery 1904 have contrasting pigmented hairs on their first legs (Wallace 1942a). And, as reported in Dondale & Redner (1978) and in this study, males of several members of the genus *Schizocosa* Chamberlin 1904 have darkly pigmented legs and or tibial bristles.

Revised by Dondale & Redner (1978), the Nearctic species of the *Schizocosa* include the 20 species recognized by Dondale & Redner plus *S. rovneri* Uetz & Dondale 1979, *S. stridulans* Stratton 1984 and *S. uetzi* Stratton 1997 and at least one undescribed species. Males of several members of the genus have conspicuous ornamentation in the form of pigmentation and/or bristles on the first legs of mature males. The ornamentation varies considerably from a complete lack of dark pigment [e.g., *S. saltatrix* (Hentz 1844), or *S. rovneri*], to slight pigment on the tibia of males

(e.g., *S. uetzi*), to concentrated tufts of bristles at one end of the tibia (e.g., *S. salsa* Barnes 1953), to bristles that extend the length of the tibia and to the metatarsus [as in *S. ocreata* (Hentz 1844) from Florida]. Indeed, it is this variability in ornamentation that makes this genus particularly interesting for behavioral and evolutionary studies. For some species, the ornamentation has proven useful in species descriptions (Uetz & Dondale 1979; Stratton 1991, 1997a) as well as in mate choice studies (McClintock & Uetz 1996; Scheffer et al. 1996; Hebets & Uetz 1999, 2000). In some cases, tibial bristles are seen in species that have similar genital morphology, e.g., *S. ocreata* and *S. crassipes*, both commonly called "the brush-legged spider", suggesting a common origin of the trait, but it is also seen in species with different genitalia [e.g. compare *S. ocreata* with *S. bilineata* (Emerton 1885)], suggesting the possibility of independent origins. Closely related species may be very divergent with respect to ornamentation, as is seen in *S. ocreata* and *S. rovneri*, two species long considered to be sibling to each other.

Ornamentation and courtship behavior in *Schizocosa* wolf spiders have been the focus of studies addressing sexual selection and signal evolution, fluctuating asymmetry and reproductive isolation (Hebets & Uetz 1999, 2000; Uetz et al. 1996, Uetz & Smith 1999; McClintock & Uetz 1996; Scheffer et al. 1996; Hebets 2003, 2005). Perhaps most surprisingly, the ornamentation on at least one species (*S. uetzi*) appears to be important in a social learning context (Hebets 2003).

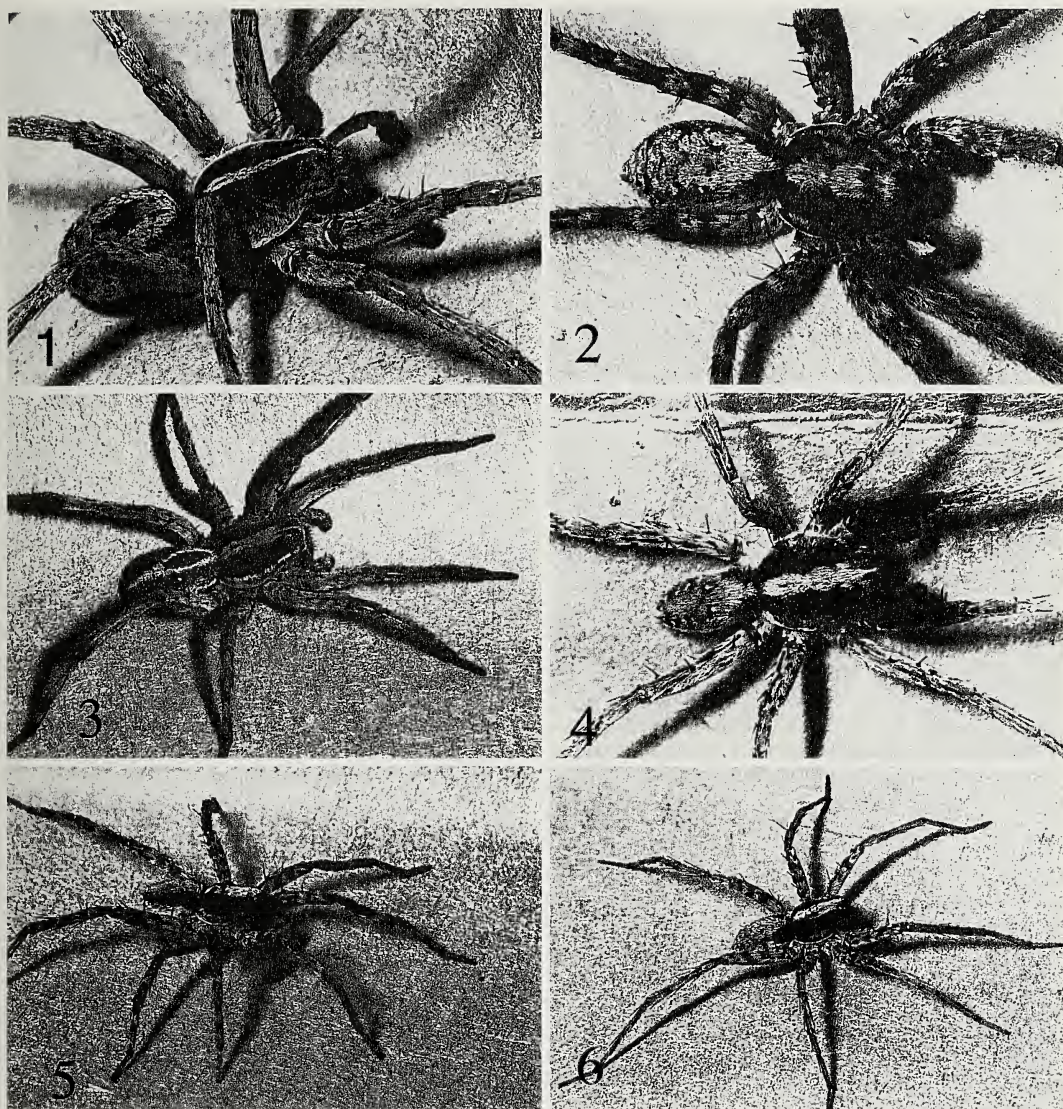
Members of the genus *Schizocosa* use a variety of modes of communication during courtship, including chemical, seismic and visual signals. In two comparative studies, Hebets & Uetz (1999, 2000) found that among six species of *Schizocosa*, females of three species exhibited a vibratory bias during courtship and three showed a visual bias. Hebets & Uetz (2000) found that in species with active visual displays but without ornamentation, an artificial increase in male ornamentation resulted in increased female receptivity. In an attempt to test the hypothesis that ornamentation evolved secondarily in this family to enhance pre-existing visual movement displays, they presented a summary of North American lycosid species which complied in-

formation on the presence/absence of ornamentation and leg waving displays. However, a phylogenetic study including more lycosid species, as in the present study, will provide a more thorough test of such a hypothesis. The mixture of ornamented species and non-ornamented species plus the complexity of courtship interactions makes the *Schizocosa* genus particularly well suited for testing ideas concerning multimodal signaling (Uetz & Roberts 2002; Hebets 2005) and the evolution of complex behaviors. The relative importance of phylogeny compared with sexual selection can be assessed with a robust phylogeny.

McClintock & Uetz (1996) presented evidence that females of *S. rovneri*, a species without leg ornamentation, showed a higher level of response to video images of conspecific males that had been visually manipulated to have tufts on their tibia and to courting heterospecific males than to controls (un-manipulated conspecific males). The preliminary phylogeny presented in their 1996 study (including 16 characters for 7 species) suggested that the female preference for ornamentations may have preceded the evolution of the ornaments themselves and thus be an example of the sensory bias hypothesis (Ryan & Rand 1993). A more complete phylogenetic study of the genus involving more species and more characters will provide a more robust test of the sensory bias hypothesis.

Here, I present the results of a comparison of the sexual ornamentation found in members of *Schizocosa* and the results of a phylogenetic study addressing the Nearctic members of this wolf spider genus. Using the results from my phylogenetic analysis, I address the following four hypotheses: 1. Ornamentation in the form of tibial bristles arose once within this genus; 2. Monophyletic groups show similarities in courtship behavior; 3. *Schizocosa ocreata* and *S. rovneri* are sibling species as was suggested by Uetz & Dondale (1979) and supported by the successful interbreeding reported in Stratton & Uetz (1986); and 4. Finally, this study presents a test of the sensory bias hypothesis presented by McClintock & Uetz (1996) that female preference seen in *S. rovneri* females for males with ornamentation preceded the evolution of ornamentation in closely related species.





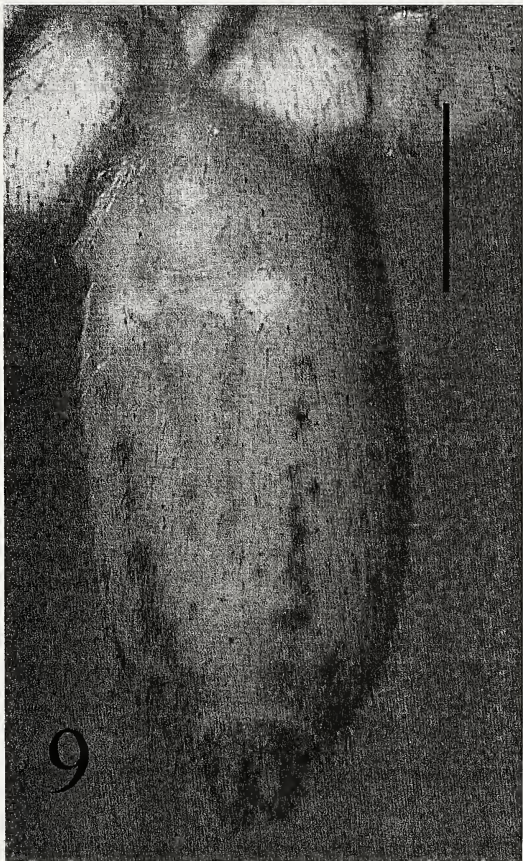
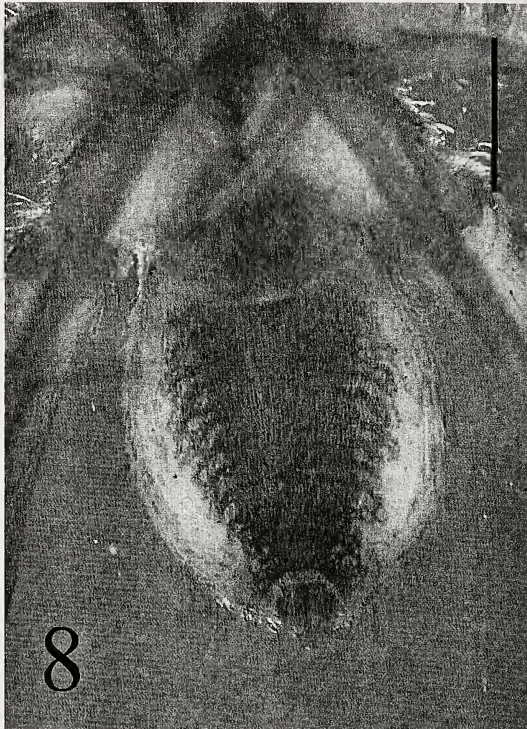
Figures 1–6.—Dorsal view of males of several of the species used in the phylogenetic study: 1. *Allocosa georgicola*; 2. *Gladicosa pulchra*; 3. *Schizocosa avida*; 4. *Schizocosa retrorsa*; 5. *Schizocosa rovneri*; 6. *Schizocosa uetzi*.

## METHODS

**Ornamentation and courtship behavior.**—As comparative data on male ornamentation and courtship behavior were not available for all species of *Schizocosa*, I initially measured the form and extent of male tibial bristles for all members of the genus and recorded the courtship behavior for selected (available) species. To document the ornamentation of each species, a lateral view of the first pair of legs for males of all species included in the study was photographed using a

dissecting microscope (Olympus SZX12) and dedicated digital camera (Olympus 750). Courtship behavior (for available species not reported in the literature) was documented by collecting subadult males and females, maintaining them in the laboratory until mature (see Stratton et al. 1996, Miller et al. 1998) and then videotaping courtship behavior. The standard protocol for recording behavior was as follows. Twenty-four hours before testing, females were fed an appropriately-sized cricket and were placed in a recording chamber







with filter paper as substrate. Males were introduced to the chamber and all interactions were recorded with either a Panasonic WD-5000 camera with Kiron 105 mm f2.8 macro-lens on standard VHS tapes or by using a Sony TRV-22 taping to a mini-DV tape. Seismic recordings were made by using a sound transducer attached to an EG&G PARC Model 113 pre-amp connecting to the video recorder. Video and seismic recordings were made for the following species, whose behavior is not yet described in the literature (summarized in Table 5): *S. avida*, *S. crassipal-pata*, *S. floridana*, *S. saltatrix*, *S. nr saltatrix*, *Gladicosa pulchra* and *Allocosa georgicola*. As courtship behavior remains unknown for several species, the behavior was not used in the parsimony analysis.

**Phylogenetic study: choice of taxa and material examined.**—There are 63 species currently listed in the genus *Schizocosa* (Platnick 2005) from all over the world. However, in this study, I chose to focus solely on the Nearctic species; explicit in the exclusion the species from the Philippines, South Africa and other localities outside of North America is the assumption that the Nearctic species are monophyletic, an hypothesis not tested in this study. However, the names of several large genera of wolf spiders (e.g., *Lycosa*, *Schizocosa* and others) were often categories of convenience rather than hypotheses of relationship for some earlier workers. For example, recent taxonomic work of New Zealand wolf spiders suggests that previous placement of species into Holarctic genera is erroneous (Vink 2002) and *Schizocosa berenice* L. Koch 1877 from Australia actually belongs in the genus *Artoria* (Framenau pers. comm.).

Additionally, I excluded species that were excluded from the genus by Dondale & Redner (1978). Many of these, e.g., *S. incerta* (Bryant 1934), *S. perplexa* Bryant 1936, *S. puebla* Chamberlin 1925, *S. tamae* (Gertsch & Davis 1940), *S. tristani* (Banks 1909) and *Avicosa ceratiola* (Gertsch & Wallace 1935) have yet to be placed in another genus but

were judged to be outside the scope of this project.

This study is thus based on direct examination of preserved specimens of the 20 *Schizocosa* species recognized by Dondale & Redner (1978), plus *S. rovnieri*, *S. stridulans*, *S. uetzi* and one undescribed species. In addition, I scored 3 populations of *Schizocosa ocreata*: one from Cincinnati, OH that has been used extensively in behavioral research (see references by Uetz, Hebets, McClintock and Stratton), a second from Central Mississippi (see Miller et al. 1998) and a third from Gainesville, Florida; and two populations of *Schizocosa crassipes*: (separate populations from Florida and Mississippi). Finally, I also scored individuals that are hybrids between *S. ocreata* (OH) and *S. rovnieri* (available from a previous study [Stratton & Uetz 1986]). Appendix 2 summarizes the specimens of the 31 taxa used and their deposition. Voucher specimens from my own collection will be deposited at the AMNH.

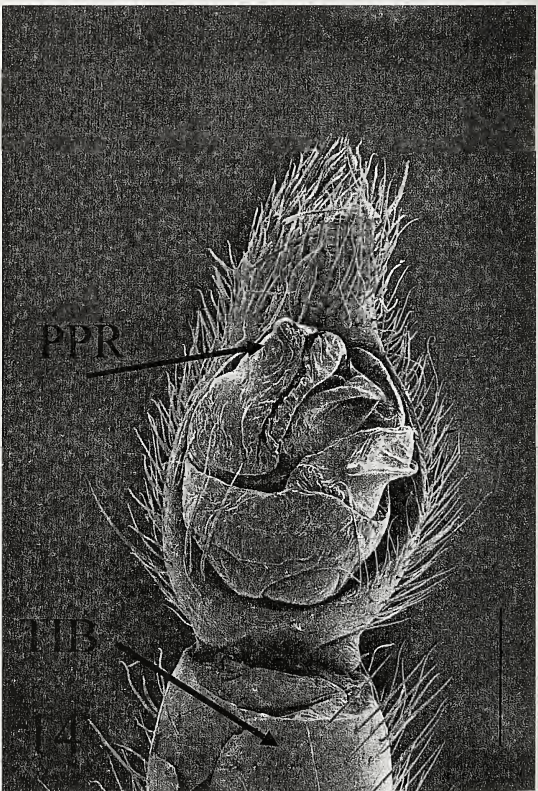
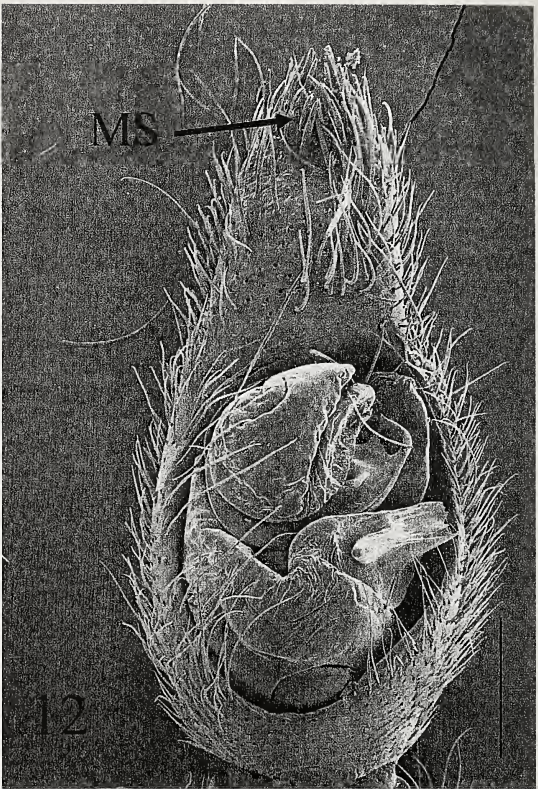
**Outgroups.**—The choice of outgroups for this study was difficult due to the incomplete knowledge of lycosid generic relationships. As the sister-group for the *Schizocosa* is not known, representatives from several different North American lycosid genera were scored and included in this analysis. *Gladicosa pulchra* (Keyserling 1877), *Allocosa georgicola* (Walckenaer 1837) and *Rabidosa rabida* (Walckenaer 1837) were chosen as outgroups for the final analysis as they all share some characters with *Schizocosa* but also have clearly distinguishing features (locality, deposition and citations for figures are given in Appendix 2). *Allocosa georgicola* has affinities to the *H. helluo* species group (Brady pers. comm.).

**Choice of characters.**—Forty nine morphological characters were found to be informative and were scored by direct examination of specimens (data matrix in Appendix 1; details of the characters are provided below). During the course of the study numerous additional characters were identified and scored

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Figures 7–10.—Ventrals of selected species: 7. Male of *Schizocosa crassipes*; 8. Male of *Schizocosa retrorsa*; 9. Female of *Schizocosa bilineata* (epigynum has been dissected); 10. Female of *Schizocosa avida*.







but discarded as too variable or uninformative. Characters were chosen by comparing the different subfamilies of Lycosidae (Dondale 1986), by screening revisions, descriptions and illustrations of other wolf spiders and by direct examination of the specimens. Figures from the following references were found to be useful: *Schizocosa* (Dondale & Redner 1978), *Trochosa* (Brady 1979); *Gladicosa* (Brady 1986); *Rabidosa* (Brady & McKinley 1994); *Geolycosa* (Wallace 1942a); *Hogna georgicola* (Chamberlin & Ivie 1944) and *Isohognia lenta* (Wallace 1942b).

As characters were treated as unordered, hypotheses of polarity are an emergent property of the analysis. Forty characters are binary; nine are multistate characters. Six of the characters are morphometric (characters 1, 17, 20, 33, 37, 39) with three being expressed as ratios (characters 17, 33, 37). To assign states for the morphometric data, I examined the data for gaps. In several cases, I opted for independent coding of variables for a given structure as opposed to coding as a multistate character with linked states to minimize assumptions of congruence (e.g., characters 21–25). However, a potential problem with this is the duplication of absences (Maddison 1993).

For the final analysis, the 49 characters were grouped in the following manner: 19 somatic characters, 14 male palpal characters, 10 female epigynal characters and six male secondary sexual characters. Several additional characters (e.g., behavioral and ecological characters) were used a posteriori and mapped onto the resulting cladograms. As data for these latter characters were not available for all species, they were not used in the parsimony analysis (Platnick et al. 1991; Maddison 1993).

**Data analysis.**—Maximum parsimony analyses were conducted using PAUP\* (Version 4.0b10) (Swofford 2002) with 1000 random starting point heuristic searches using Stepwise-addition option and 1000 random taxon addition sequences and tree-bisection-reconnection (TBR) branch swapping. The re-

sults from other swapping algorithms were compared to TBR branch swapping. All characters were unordered and several weighting schemes were examined. The trees were rooted by setting the three non-congeners as outgroups. Characters were mapped using MacClade Version 3.0 (Maddison & Maddison 1992). The degree of internal support for the resulting clades was estimated using bootstrap analysis (using 100 random addition sequence replicates and 100 bootstrap replicates).

**Weighting options.**—The data set was first analyzed with all characters weighted equally. However, preliminary analyses suggested there was little phylogenetic signal in the somatic characters. Subsequent analysis investigated several different weighting options including reweighting with the rescaled consistency index as well as weighting the genitalic characters more heavily. As most modern students of wolf spiders use genitalic characters extensively in revisions and descriptions (Dondale & Render 1978, 1990; Brady 1962, 1979, 1986; Brady & McKinley 1994) and because wolf spiders appear to be very conservative in their somatic morphology, I favor the trees produced by weighting the genitalic characters more heavily. In the final analysis, I used the following weighting scheme: somatic characters weighted as “2”; genitalic characters weighted as “3” and secondary sexual characters weighted as “1.” Finally, as I was interested in the evolution of secondary sexual characters, I compared trees produced by excluding secondary sexual characters with trees including those characters.

**Description of characters.**—*Somatic characters:* 1. Body size: 0 = medium; 1 = large; 2 = small. Measurements of the carapace were made as the best representation of body size, as unlike the spider's abdomen, it does not vary with a recent meal. Carapace length and width were measured dorsally using an ocular micrometer. The ratio of the carapace length to width was similar across all species used in this study (Table 1). Carapace length

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Figures 11–14.—Left pedipalps of males from selected species of *Schizocosa*. Localities are indicated in Appendix 2: 11. *S. avida*; 12. *S. retrorsa*; 13. *S. saltatrix*; 14. *S. duplex*. ELL = ear-like lobe, IPE = intromittent portion of embolis, MA = median apophysis, TA = terminal apophysis. Scale lines = 500  $\mu$ m.

Table 1.—Body size (carapace length, carapace width and ratio of length/width) of male and female *Schizocosa* and outgroups used in this study. All measures are in mm. Measures of female *S. aulonia*, and *S. maxima* are from Dondale & Redner (1978), measures from *S. salsa* are from Barnes (1952).

Species	Male			Female		
	Length	Width	L/W	Length	Width	L/W
<i>S. aulonia</i>	4.0	2.8	1.4	5.5	4.0	1.4
<i>S. avida</i>	4.8	3.6	1.3	6.8	5.0	1.4
<i>S. bilineata</i>	2.9	2.1	1.4	3.5	2.5	1.4
<i>S. cespitum</i>	3.6	2.6	1.4	4.2	3.0	1.4
<i>S. chiricahua</i>	4.2	3.0	1.4	3.8	2.5	1.5
<i>S. communis</i>	4.6	3.4	1.4	4.0	3.0	1.3
<i>S. crassipalpata</i>	3.1	2.3	1.3	3.1	2.2	1.4
<i>S. crassipes</i> (FL)	3.2	2.6	1.2	3.8	2.7	1.4
<i>S. crassipes</i> (MS)	3.2	2.4	1.3	3.4	2.6	1.3
<i>S. duplex</i>	3.2	2.5	1.3	3.2	2.4	1.3
<i>S. floridana</i>	2.6	2.0	1.3	3.1	2.5	1.2
<i>S. humilis</i>	3.1	2.3	1.3	3.6	2.6	1.4
<i>S. maxima</i>	9.0	7.7	1.2	12.1	9.0	1.3
<i>S. mccooki</i>	3.7	2.8	1.3	4.2	3.2	1.3
<i>S. mimula</i>	4.0	2.9	1.4	4.2	2.8	1.5
<i>S. minnesotensis</i>	4.6	3.2	1.4	4.9	3.6	1.4
<i>S. ocreata</i> (OH)	3.8	2.8	1.4	4.1	3.2	1.3
<i>S. ocreata</i> (MS)	3.7	2.7	1.4	4.5	3.4	1.3
<i>S. ocreata</i> (FL)	4.0	3.0	1.3	4.2	3.3	1.3
<i>S. retrorsa</i>	3.7	2.7	1.4	3.4	2.7	1.3
<i>S. rovneri</i>	3.4	2.6	1.3	3.7	3.0	1.2
<i>S. salsa</i>	4.1	3.0	1.4	4.1	2.9	1.4
<i>S. saltatrix</i>	3.7	3.0	1.2	3.6	3.0	1.2
<i>S. S. sp. nr. saltatrix</i>	4.0	3.2	1.3	3.6	2.8	1.3
<i>S. segregata</i>	3.0	2.2	1.4	3.2	2.2	1.5
<i>S. stridulans</i>	3.2	2.4	1.3	3.0	2.3	1.3
<i>S. uetzi</i>	3.6	2.8	1.3	3.7	3.0	1.2
<i>S. ocr</i> × <i>rov</i> hybrids	3.8	3.1	1.2	4.3	3.5	1.2
<i>A. georgicola</i>	8.0	6.9	1.2	10.0	7.5	1.3
<i>G. pulchra</i>	6.0	4.5	1.3	6.4	5.0	1.3
<i>R. rabida</i>	7.8	5.9	1.3	9.8	7.4	1.3

as states: carapace length  $\geq 4.5$  mm for “large”, carapace length between 3.5 and 4.5 mm for “medium” and carapace length  $\leq 3.5$  mm for “small”.

2. Median band (MB) width: 0 = narrow; 1 = medium; 2 = broad. The median band is a light band on the dorsal surface of the carapace. It may be a thin line (as in *A. georgicola*, Fig. 1, which is distinctly thinner than the posterior median eyes) or it may be “broad,” or as broad as the posterior median eyes (as in *G. pulchra*, Fig. 2, and members of *Schizocosa*, Figs. 3–6). A medium-sized median band is present in *Rabidosa* spp. (Brady and McKinley 1994, p. 140, figs. 1–5).

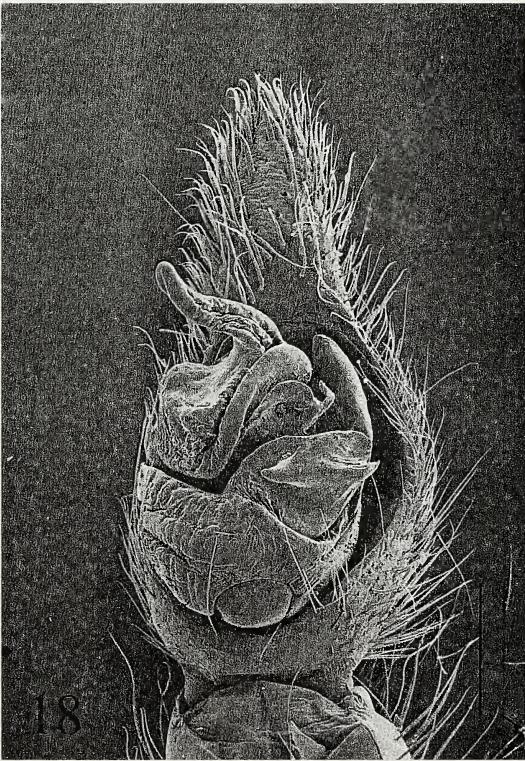
3. Median band edges: 0 = straight; 1 = not straight. The edges of the median band can

be straight as in Fig. 1, 3, 5, 6), or can have some constriction as is seen in *G. pulchra* or *S. retrorsa* Banks 1911 (Figs. 2, 4).

4. Submarginal band (SMB), edges: 0 = absent; 1 = smooth; 2 = wavy or spots. The submarginal band is a light band near the edges of the carapace. It can be present as either a relatively smooth band (as in *S. avida* and *S. rovneri*, Figs. 3, 5) or diffuse or lacking as in *A. georgicola* (Fig. 1). In *S. retrorsa* (Fig. 4) the SMB consists of spots at the edges of the carapace.

5. Submarginal band, size: 0 = absent; 1 = narrow; 2 = broad. In most species of *Schizocosa*, the SMB is narrow or absent. In *Rabidosa* spp. (Brady & McKinley 1994, figs. 1–5, p. 140) and in *S. salsa*, the SMB is wider





Figures 15–18.—Pedipalps of males from selected populations of *Schizocosa ocreata* and *S. crassipes*. Localities as indicated in Appendix 2: 15. *S. ocreata* (FL); 16. *S. ocreata* (MS); 17. *S. crassipes* (FL); 18. *S. crassipes* (MS). Scale lines = 500  $\mu$ m.



than the median band and scored as broad (Barnes 1953, fig. 16).

6. Heart mark (HM): 0 = absent or faint; 1 = strong. In some Lycosinae, the heart mark is a darkened region on the dorsum of the abdomen where the heart is located (e.g. *A. georgicola* & *S. avida*, Figs. 1, 3).

7. Light bands on abdomen: 0 = absent; 1 = present. In some cases, the HM is apparently accentuated by the presence of white lines on either side of the HM (as in *S. avida*, Fig. 3).

8. Sternum color: 0 = yellow or light brown; 1 = orange, dark brown or black.

9. Bands on sternum: 0 = absent; 1 = present. Sternum bands, as used for this study, are longitudinal bands that extend from the anterior to the posterior end of the sternum.

10. Shield on venter: 0 = absent; 1 = present. When present, this is a light patch on black background on the venter of the animal as in *S. avida* (Fig. 10). The shape of the light patch varies between individuals from the same geographic area (Stratton, unpublished data).

11. Ventral color of abdomen: 0 = light or mostly light; 1 = black or mostly black; 2 = light shield on black. Light or mostly light is as in *S. crassipes* or *S. bilineata* (Emerton 1885) (Figs. 7, 9); black or mostly black, as in *S. retrorsa* (Fig. 8); and light shield on black as in *S. avida* (Fig. 10).

12. "V" on venter: 0 = absent; 1 = present. The "V" is formed by dark pigmented spots near the lateral edges of the venter (*S. bilineata*, Fig. 12). The inner "V" on *S. bilineata* is not pigmented and originates in points of muscle attachment.

13. Spots on venter: 0 = absent; 1 = present. Similar to character 12 but in some cases and in *S. crassipes*, the spots on the venter are scattered.

14. Color of coxae: 0 = light to light brown; 2 = dark brown.

15. Color of coxae relative to the femur: 0 = same as femora; 1 = lighter than femur; 2 = darker than femur.

16. Dark lines on chelicerae: 0 = absent; 1 = present. When present, these are vertical lines running the length of the chelicerae when viewed from the front.

17. Relative tibial length of males: 0 = short to medium; 1 = long. Examination of the specimens suggested that some of the spe-

cies had particularly stout legs, others were relatively long-legged, while many fell between these extremes (also noted by Krones-tedt 1990). Since there was a wide range of body sizes in the examined species, I took a relative measure for leg length. Tibia 1 (measured with an ocular micrometer along the dorsal edge) divided by the carapace length was taken as the relative measure of leg length that could be potentially informative. Values for this ratio ranged from 0.5 for *S. cespitum* Dondale & Redner 1978 to 0.92 for *S. salsa* (Table 2). Gaps were identified by examination of the distribution of values. These data were first collapsed into a binary coding (0 = short to medium,  $tl/cl \leq 0.71$  and 1 = long  $tl/cl > 0.71$ ). The data were also scored as a multistate character with any gap  $> 0.03$  used to define states. With this coding there were seven character states. During character exploration, analyses were run both ways; this character was judged to have a large amount of homoplasy and in the final analysis, I used the binary coding.

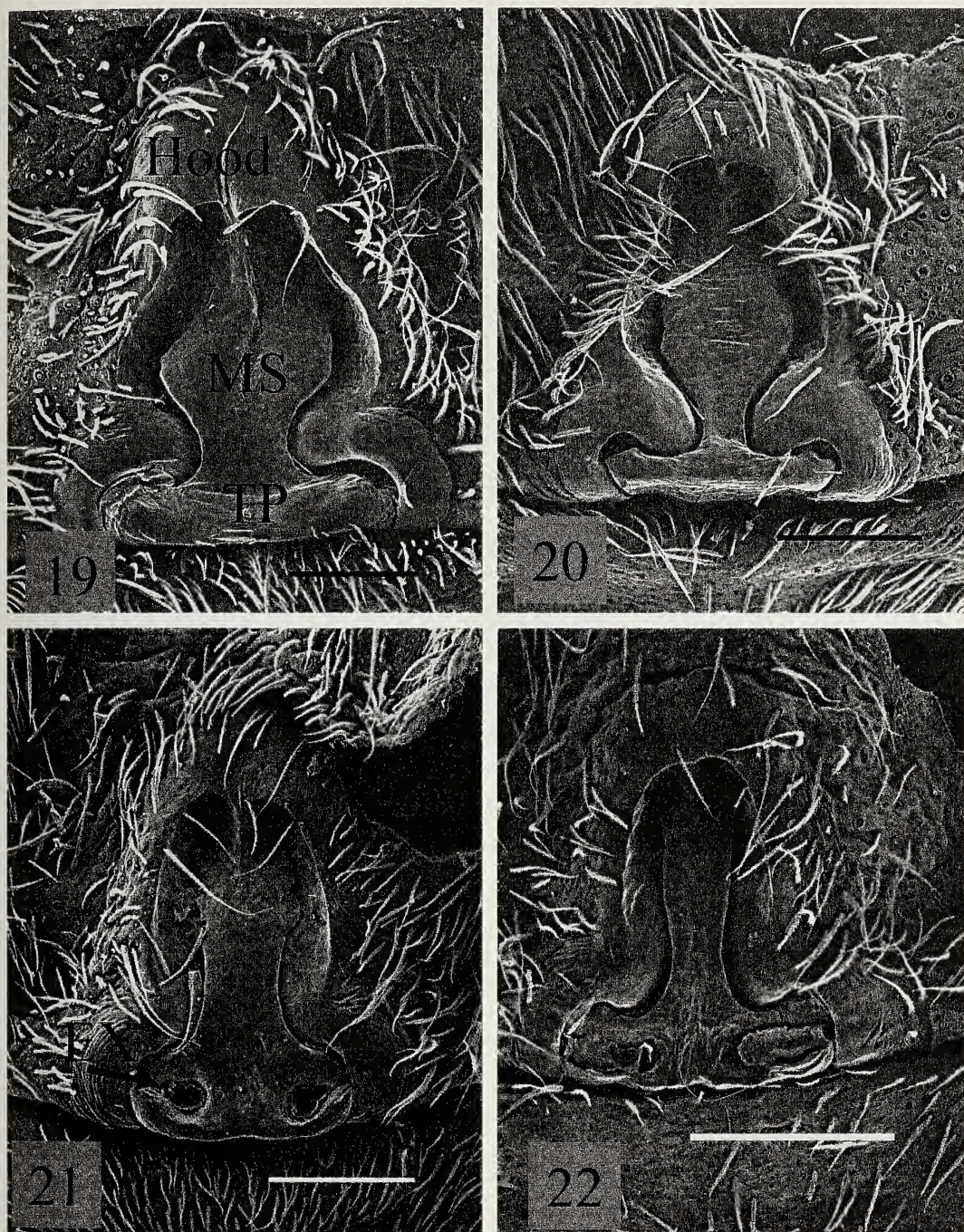
18. Femur I annulations (male): 0 = absent; 1 = present.

19. Femur II-IV annulations (male): 0 = absent; 1 = present.

*Male palpal characters:* Palpal structures have been successfully employed in spider taxonomy and have been central in wolf spider revisions. Eberhard (1994) suggested that the complexity of genitalic characters has been shaped by sexual selection. The complexity of the pedipalps has made determination of homologies of structures between families difficult. Even within a single family, such as the Lycosidae, terms have been used in a variety of ways. I here follow the terminology suggested by Dondale & Redner (1978) with comparisons to Brady (1986) and have focused primarily on structures that aid in the determination of species.

The cymbium of the tarsus (terminal segment) forms the body of the tarsus of the pedipalp and holds the sclerites (genital bulb) involved in copulation. At the tip of the cymbium there may be macrosetae (MS, Fig. 12), which function to hold the pedipalp in place while the spider stridulates [e.g., *S. saltatrix* and *R. rabida* (Walckenaer 1837), Rovner 1975]. The genital bulb is an interconnected assemblage of sclerites and distensible sacs (the hematodocha). During copulation,





Figures 19–22.—Epigyna of selected species. Localities as indicated in Appendix 2: 19. *S. avida*, 20. *S. retrorsa*, 21. *S. crassipes* (MS); 22. *S. duplex*. MS = median septum, TP = transverse piece. Scale lines = 250  $\mu$ m.

the hematodocha becomes visible as an expanding sac of haemolymph. The cymbium is attached to the palpal tibia (Tib, Fig. 14).

Located on the genital bulb is the terminal

apophysis (TA, Fig. 11) which in *Schizocosa* is a small, free sclerite near the base of the intromittent portion of the embolus (IPE) (Figs. 11–18; see also Dondale & Redner



Table 2.—Tibial length and relative tibial length (tibial L/carapace L) of males of *Schizocosa* and outgroups. All measures are in mm.

Species	Male		
	Cara length	Tibia length	Tibial L/ Cara L
<i>S. aulonia</i>	4.0	2.5	0.61
<i>S. avida</i>	4.8	3.6	0.75
<i>S. bilineata</i>	2.9	2.0	0.67
<i>S. cespitum</i>	3.6	2.0	0.50
<i>S. chiricahua</i>	4.2	2.5	0.60
<i>S. communis</i>	4.6	2.5	0.68
<i>S. crassipalpata</i>	3.1	1.8	0.57
<i>S. crassipes</i> (FL)	3.2	2.8	0.85
<i>S. crassipes</i> (MS)	3.2	2.5	0.84
<i>S. duplex</i>	3.4	2	0.66
<i>S. floridana</i>	2.6	1.5	0.58
<i>S. humilis</i>	3.1	1.8	0.58
<i>S. maxima</i>	9.0	6.4	0.71
<i>S. mccooki</i>	3.7	2.7	0.74
<i>S. mimula</i>	4.0	2.7	0.68
<i>S. minnesotensis</i>	4.6	2.4	0.51
<i>S. ocreata</i> (OH)	3.8	3	0.78
<i>S. ocreata</i> (MS)	3.7	2.6	0.71
<i>S. ocreata</i> (FL)	4.0	2.6	0.65
<i>S. retrorsa</i>	3.7	2.6	0.71
<i>S. royneri</i>	3.4	2.6	0.76
<i>S. salsa</i>	4.1	3.8	0.92
<i>S. saltatrix</i>	3.7	2.5	0.67
<i>S. S. sp. nr. saltatrix</i>	4.0	2.5	0.62
<i>S. segregata</i>	3.0	1.8	0.59
<i>S. stridulans</i>	3.2	2.4	0.75
<i>S. uetzi</i>	3.6	3.0	0.83
<i>S. ocr</i> × <i>rov</i> hybrids	3.8	2.6	0.68
<i>A. georgicola</i>	8.0	5.5	0.68
<i>G. pulchra</i>	6.0	4.8	0.83
<i>R. rabida</i>	7.8	7.0	0.89

1978). In *Gladicosa* and *Hogna*, the TA is an elongate structure that parallels the embolus and may assist in the proper placement of the IPE in the female epigynum (see Brady 1986, p. 314, fig. 41). Also clearly visible is the median apophysis (MA, Figs. 11–18) which is directed retrolaterally and has a sinuous channel on the dorsal surface, which are defining characters of the subfamily Lycosinae. A spur of the median apophysis engages the hood of the female epigynum during copulation. The palea is a partly sclerotized pad at the distal end of the genital bulb that sometimes bears processes or extensions (PPR) (Figs. 14–18). An ear-like lobe (ELL, Fig. 11) is also present in *Schizocosa* and *Gladicosa* (called the con-

ductor by Dondale & Redner 1978). The base of the cymbium holds the scraper portion of the stridulatory structure, not visible in the ventral view shown. The tip of the tibia has the file of the stridulatory organ, found only in mature males.

20. Palpal tibia: 0 = length > width; 1 = length ≤ width. Measured ventrally using an ocular micrometer. For some species (i.e., *A. georgicola*), the tibia of the pedipalp is long and thin (nearly twice as long as wide) (Table 3). For others, as in *S. ocreata* (FL), it is very stout and is wider than long (Table 3). A short, stout tibial palp is probably related to muscle mass needed for stridulation during courtship (Rovner 1975). Although all members of the *Schizocosa* and outgroups included here possess a stridulatory organ, for some, palpal drumming is an important component of the courtship behavior (Table 5; see discussion below).

21. Terminal apophysis (TA): 0 = present; 1 = small or absent.

22. Terminal apophysis, size: 0 = elongate; 1 = small or absent. The TA in *Schizocosa* is generally present but relatively small compared to that in the outgroups, *A. georgicola* and *G. pulchra* (Figs. 11–18; compare to, Brady 1986, p. 314, fig. 41), where the TA is an elongate structure.

23. Terminal apophysis with slight arch: 0 = absent; 1 = present. The TA may form a slight arch, as seen in Figs. 15 and 16.

24. Terminal apophysis, with tear-drop shape: 0 = absent; 1 = present. See fig. 13 in Dondale & Redner (1978).

25. Terminal apophysis as inverted triangle: 0 = absent; 1 = present.

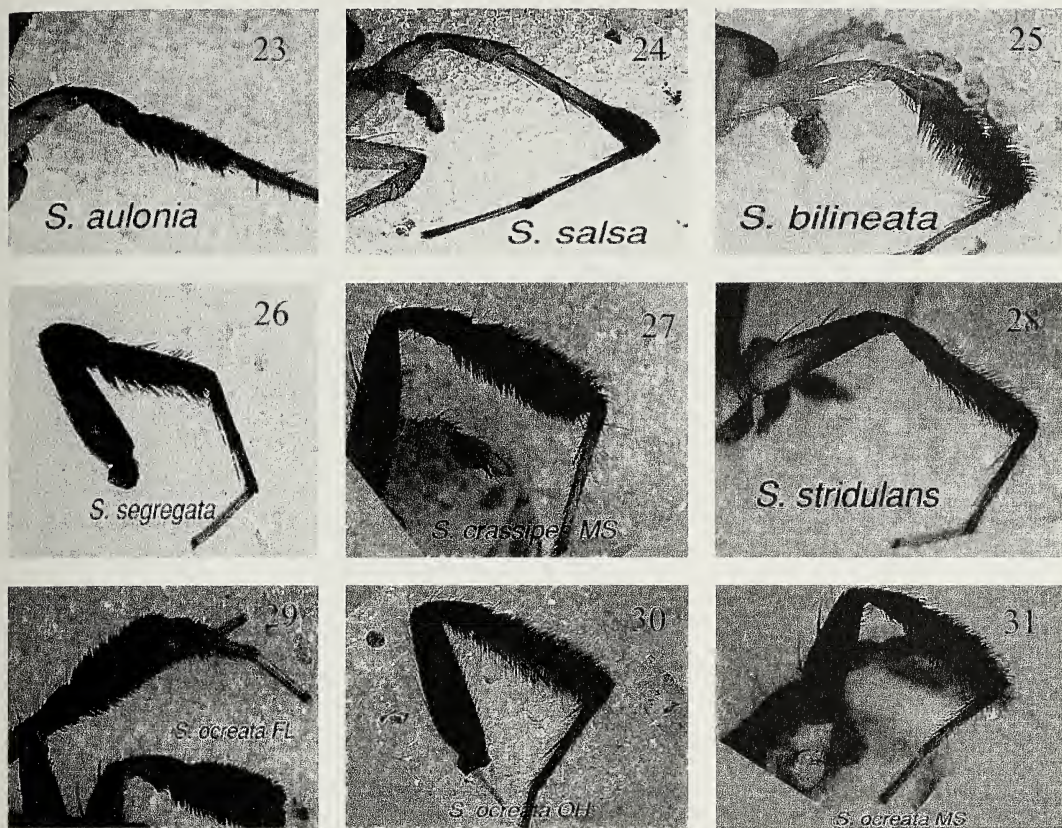
26. Embolus, basic shape: 0 = hair-like; 1 = sword-like. All pedipalps in Figs. 11–18 show a hair-like embolus. The sword-like embolus is found in *Gladicosa*, whose name refers to a sword (Brady 1986, p. 314, fig. 41).

27. Width of intromittent portion of embolus (IPE, Fig. 11): 0 = thin; 1 = stout.

28. Palea of pedipalp with triangular process: 0 = absent; 1 = present. In a few species, notably *S. duplex*, *S. saltatrix* and an undescribed species, the pedipalp has a triangular shaped process (Fig. 13, 14).

29. Palea of pedipalp with finger-like process: 0 = absent; 1 = present. A finger-like process (PPR) is shown in Fig. 15–18. During copulation this process pushes against the cu-





Figures 23–31.—Shape and size of tibial bristles in all taxa with the tibial bristles in the Nearctic *Schizocosa*: 23. *S. aulonia*; 24. *S. salsa*; 25. *S. bilineata*; 26. *S. segregata*; 27. *S. crassipes* (MS); 28. *S. stridulans*; 29. *S. ocreata* (FL); 30. *S. ocreata* (OH); 31. *S. ocreata* (MS).

ticle to the side of the female epigynum (Stratton, unpublished data).

30. Number of macrosetae: 0 = few (4–9); 1 = many (10 or more). The macrosetae can be found on the tip of the cymbium. Often there is a dense cluster, but sometimes they are much fewer and easily counted.

31. Long hair-like setae between macrosetae and genital bulb: 0 = absent; 1 = present.

32. Relative size of macrosetae: 0 = thin; 1 = stout or very stout.

33. Cymbium (tarsus) of pedipalp, length to width: 0 = short to regular; 1 = long and thin. Measured ventrally with an ocular micrometer (Table 3). As with other quantitative characters, the data were examined for gaps. During character analysis, this character was first scored as a multistate character but for the final analysis, it was treated as a binary character. The species that showed palpal drumming during courtship had relatively long, thin

pedipalps (e.g. *S. avida*, *S. retrorsa*, *S. mccoocki*, and *S. communis*; Tables 3 & 5).

*Female epigynal characters:* The prominent features of the female epigynum include the well sclerotized median septum (MS, Figs. 19–22), the posterior transverse piece (TP, Fig. 19). The edges of the median septum can be flared at the posterior end, parallel, or can be widest at the center. The anterior end of the median septum has a funnel-like hood (Hood, Fig. 19) that generally is double but is single in *S. bilineata* and *S. crassipalpa* Roewer 1951. The median apophysis of the male “catches” on the hood of the female epigynum during the first stages of copulation; this serves to brace the pedipalp and immediately following the engagement of the MA with the hood, one can see the expansion of the hematodocha of the male pedipalp (Dondale & Redner 1978; Stratton, unpublished data). The depth of the hood varies between species and



Table 3.—Length, width and length/width of tibia and tarsus of pedipalp for *Schizocosa* and outgroups. All measures in mm.

Species	Tibia of palp			Tarsus of palp		
	Length	Width	L/W	Length	Width	L/W
<i>S. aulonia</i>	0.2	0.2	1.2	1.1	0.5	2.0
<i>S. avida</i>	0.7	0.5	1.5	0.9	0.4	2.4
<i>S. bilineata</i>	0.4	0.4	1.0	0.9	0.5	1.8
<i>S. cespitum</i>	0.5	0.4	1.3	1.2	0.6	2.1
<i>S. chiricahua</i>	0.5	0.4	1.4	1.2	0.6	2.1
<i>S. communis</i>	0.6	0.4	1.4	1.3	0.6	2.1
<i>S. crassipalpata</i>	0.4	0.3	1.1	0.9	0.5	1.7
<i>S. crassipes</i> (FL)	0.3	0.3	1.0	0.7	0.4	1.9
<i>S. crassipes</i> (MS)	0.6	0.5	1.1	1.1	0.6	1.9
<i>S. duplex</i>	0.4	0.5	0.9	1.0	0.5	1.9
<i>S. floridana</i>	0.5	0.4	1.3	0.9	0.5	1.9
<i>S. humilis</i>	0.5	0.5	1.1	1.0	0.6	1.7
<i>S. maxima</i>	0.4	0.3	1.3	1.0	0.6	1.6
<i>S. mccooki</i>	0.6	0.4	1.4	1.2	0.6	2.1
<i>S. mimula</i>	0.3	0.2	1.5	1.1	0.6	2.1
<i>S. minnesotensis</i>	0.7	0.5	1.4	1.5	0.7	2.2
<i>S. ocreata</i> (OH)	0.6	0.6	1.0	1.4	0.8	1.9
<i>S. ocreata</i> (FL)	0.5	0.6	0.8	1.3	0.8	1.7
<i>S. ocreata</i> (MS)	0.6	0.6	1.0	1.3	0.7	1.8
<i>S. retrorsa</i>	0.6	0.4	1.3	1.3	0.6	2.1
<i>S. royneri</i>	0.6	0.6	0.9	1.3	0.7	1.8
<i>S. salsa</i>	0.7	0.5	1.3	1.3	0.6	2.3
<i>S. saltatrix</i>	0.7	0.6	1.1	1.1	0.6	1.8
<i>S. sp. nr saltatrix</i>	0.7	0.6	1.1	1.2	0.7	1.8
<i>S. segregata</i>	0.4	0.4	1.1	0.9	0.5	1.9
<i>S. stridulans</i>	0.5	0.5	1.0	1.1	0.6	1.8
<i>S. uetzi</i>	0.6	0.6	1.1	1.3	0.7	1.9
<i>S. ocr. × rov hybrids</i>	0.6	0.6	1.0	1.1	0.6	1.8
<i>A. georgicola</i>	1.6	0.8	1.9	2.7	1.1	2.4
<i>G. pulchra</i>	1.0	0.6	1.6	2.1	1.1	1.9
<i>R. rabida</i>	1.7	0.8	2.1	2.9	1.1	2.6

is much deeper in *G. pulchra* and *A. georgicola* than most of the *Schizocosa* species (Table 4; compare Figs. 19–22).

The transverse piece (TP) in *Schizocosa* is either truncate as in *S. avida* and *S. retrorsa* (Figs. 19 & 20) or has excavations (Figs. 21 & 22). The excavations can be located at the lateral edges of the transverse piece as seen in *S. duplex* (Fig. 22) and *S. saltatrix*, or the excavations can be almost touching near the center of the transverse piece as seen in *S. uetzi* (see Stratton 1997a). More often, the location of the excavations are somewhat between these extremes.

In lycosids, the copulatory opening is near lateral edges of the transverse piece and the genital opening (where the eggs leave the genital tract) is in the epigastric furrow. When the

female genitalia are dissected and the dorsal side is examined, the spermathecae are the dominant structures (see Stratton 1997, fig. 5).

34. Edges of median septum (MS): 0 = MS widest at center; 1 = edges of MS parallel; 2 = MS widest at base. For MS widest at center, see Figs. 19 and 20 (*S. avida* and *S. retrorsa*). *Schizocosa duplex* provides an example of the parallel edges (Fig. 22) while *S. crassipes* shows a MS widest at its base (Fig. 21).

35. Excavations on transverse piece of epigynum: 0 = absent; 1 = present; see Figs 19–22.

36. Separations of excavations: 0 = absent; 1 = widely separated with excavations near lateral edge; 2 = intermediate in placement; 3 = narrowly separated. The excavations were considered widely separated if a hypothetical



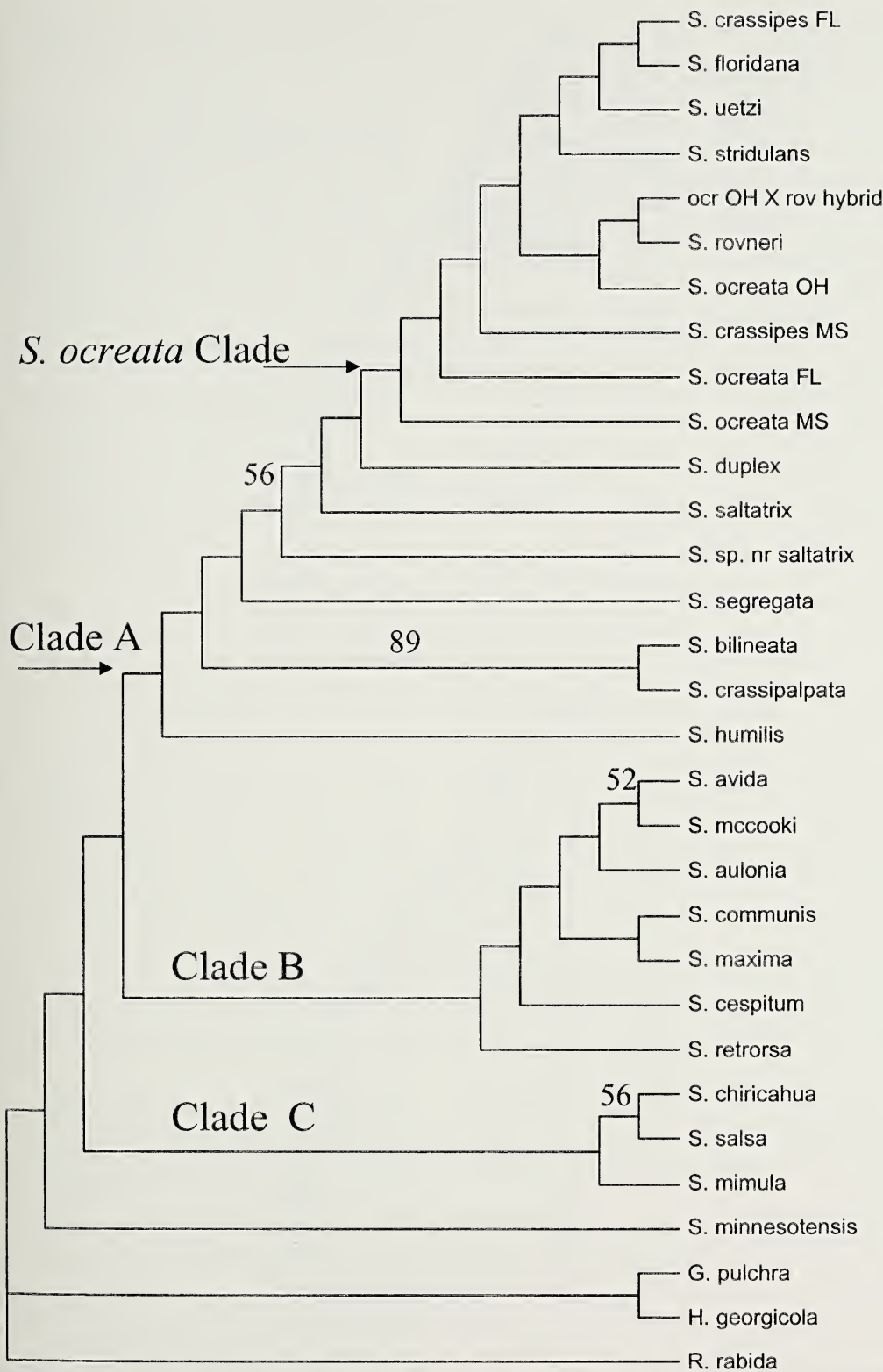


Figure 32.—Single most parsimonious tree from heuristic searches including all taxa, excluding secondary sexual characters and applying preferred weighting (somatic characters = “2,” genitalic characters = “3.” The tree shows clades A, B, & C as well as the *S. ocreata* clade. Bootstrap values above 50% are shown.

additional excavation could fit between the excavations.

37. Ratio of median septum to transverse piece: 0 =  $MS/TP \leq 0.72$ ; 1 =  $MS/TP < 1.179$ ; 2 =  $MS/TP < 1.357$ ; 3 =  $MS/TP \leq 1.52$ ; 4 =  $MS/TP = 1.583$ . As with other quantitative characters, the ratio of MS to TP was sorted, graphed and examined for gaps. The ratio of the overall length to width was also examined but for this latter ratio, there were no clear gaps.

38. Epigynal hood, single or double: 0 = double; 1 = single. Figs 19–22 show a double hood; a single hood seen in *S. bilineata* and *S. crassipalpata* (Dondale & Redner 1978; figs. 47 & 49).

39. Depth of epigynal hood: 0 = deep; 1 = shallow. See Table 4.

40. Spermathecae, shape: 0 = rounded; 1 = elongate; 2 = pointed.

41. Spermathecae texture: 0 = smooth; 1 = bumpy. The “bumpy” texture was visible with light microscopy; the function of these bumps is unknown.

42. Copulatory tube: 0 = simple; 1 = complex. The copulatory ducts for *Schizocosa* (Dondale & Redner 1978; e.g. figs. 28, 32 & 37) have a single elbow and were scored as simple. The copulatory duct in *R. rabida* (Brady & McKinley 1994; fig. 13) is convoluted and was scored as complex.

43. Pigment around the epigynum: 0 = absent; 1 = present. In some species, there is a distinct “box” of dark pigment surrounding the epigynum.

Male secondary sexual characters (ornamentation): Male secondary sexual characters include both pigmentation on the first legs and bristles or brushes, primarily on the tibia of legs I. Work by Stratton & Uetz (1986) showed that through hybridization of *S. ocreata* and *S. rovneri* these characters are inherited independently.

44. Femur I with dark stripe: 0 = absent; 1 = present.

45. Femur I with dark pigment: 0 = absent; 1 = present.

46. Femur II–IV with longitudinal stripe: 0 = absent; 1 = present.

47. Presence of bristles on tibia: 0 = absent; 1 = present (see Figs. 23–31 for examples of species with bristles).

48. Dark pigment covering tibia I: 0 = absent; 1 = present.

49. Metatarsus I bristles: 0 = absent; 1 = present (e.g., *S. ocreata*, FL, Fig. 29).

## RESULTS

**Sexual ornamentation.**—Sexual ornamentation in the Nearctic genus *Schizocosa* consists of pigmentation on all or part of the legs I of mature males and/or bristles which are generally limited to all or part of the tibia of legs I. Dark pigmentation can be limited to the femur of leg I (as in *S. retrorsa*, Fig. 4), or to part of the femur and extending to the tibia (as in *S. stridulans*) (Fig. 28), or may be limited to the tibia (as in *S. uetzi*, Fig. 35), or extend from the patella to the metatarsus (as in *S. floridana* Bryant 1934, Fig. 35). In some cases, such as *S. humilis* and *S. retrorsa*, the dark pigmentation of the femur contrasts sharply with light hairs found on the tibia. Dark pigmentation can occur without bristles, as is seen in *S. retrorsa*, *S. uetzi* and in the outgroup, *Rabidosa rabida*.

When present, the bristles are always associated with the tibia of legs I of mature males but may be found only on the distal end of the tibia (as in *S. salsa*, Fig. 24), may extend to much of the metatarsus, as is seen in *S. ocreata* from Florida (Fig. 29), or may be limited to the tibia as is seen in *S. bilineata* (Fig. 25). In *S. aulonia* Dondale 1969 and *S. segregata*, the bristles are longest along the ventral side of the tibia (Figs. 23, 26), while in *S. crassipes* and *S. ocreata* (Figs. 27, 29, 30, 31), the bristles extend both dorsally and ventrally, providing a large rectangular appearance when viewed from the side. In general, the bristles are largest when viewed from the side, at eye-level with the spider. A discussion of the phylogenetic distribution of the bristles follows the presentation of the preferred phylogeny.

**Comparison of courtship behavior.**—Courtship behavior for 20 of the 31 taxa represented in this study has been documented (summarized in Table 5), including all members of the *S. ocreata* clade, as well as the hybrids between *S. ocreata* (OH) and *S. rovneri*. All species studied to date show chemosignaling by males in the presence of females or female silk (indicating the presence of chemical signals) and males of all species produce seismic signals either by stridulation by the male palp (first described by Rovner 1975), palpal drumming (Stratton & Lowrie

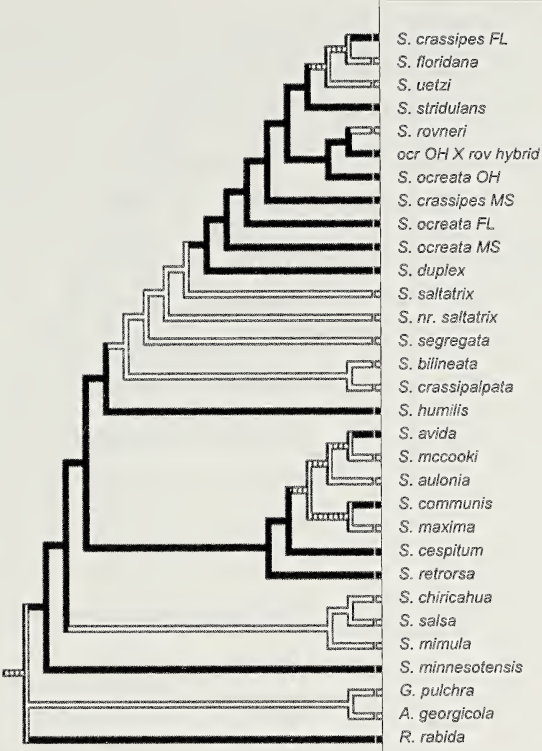


Femur with dark pigment (male)

□ absent

■ present

▨ equivocal



Dark pigment covering tibia (males)

□ absent

■ present

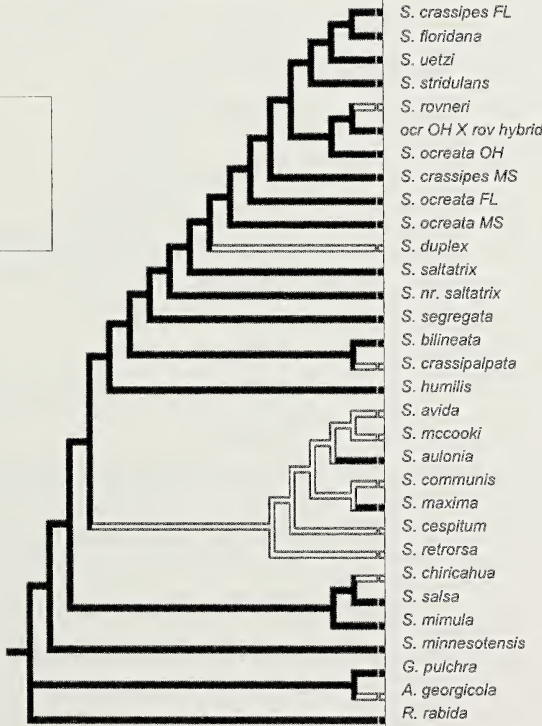


Figure 33.—Mapping of the ornamentation characters “pigment on femur” and “pigment on tibia,” seen in mature males on the preferred phylogeny.

1984; Hebets et al. 1996), body vibration or some combination of these (Table 5). Many species (but not all) also have some movement that appears to be a visual signal produced by males during courtship. Several species incorporate an arch of legs 1 (scored as a “+” in Fig. 36). For example, this is seen in *S. avida*, and *S. saltatrix* as well as *S. ocreata* (OH) (Table 5). Other species have movements that appear to be more intense visual signals. For example, *S. retrorsa* males have a vigorous leg 1 wave that is associated with courtship (Hebets et al. 1996), and *S. ocreata* (FL) has a bilateral double arch of the first pair of legs. These more overt visual signals are scored as “++” in Fig. 36. One species that apparently lacks visual signals is *S. duplex*. All populations of *S. ocreata* and *S. crassipes* have leg arching plus either leg waving or tapping. When the different populations of *S. crassipes* were compared, each population showed similar elements of courtship but differed in the proportion of time spent doing each behavior and in the sequences of behavior (e.g., Miller et al. 1998; Germano et al., unpublished data). Kaston (1936) included *S. bilineata* in his comparative courtship study but he did not see any behaviors preceding copulation in this species. Finally, the behavior of several species remains unknown and it is hoped that this study may stimulate interest in the behavior and ecology of these species.

**Results of phylogenetic analysis.**—Parsimony analysis with all characters weighted equally and trees not rooted resulted in very little resolution of clades. The agreement subtree for these trees did not include the three outgroups, suggesting their position in the tree was not stable. When the preferred weighting option was applied and the trees rooted with the three outgroups, there was more resolution. A single most parsimonious was tree resulted from the analysis with the secondary sexual characters excluded and is the preferred tree presented here (Fig. 32; bootstrap values above 50% shown on figures; 570 steps, Consistency Index = 0.271, Retention Index = 0.567, Homoplasy Index = 0.729). When secondary sexual characters were included, a consensus of seven trees had 578 steps (Consistency Index = 0.265, Homoplasy Index = 0.735 and Retention Index = 0.549) and when compared to the preferred tree, differed only

Table 4.—Epigynal measures including total length of epigynum, and width of epigynum, the ratio of epigynal length/width, and depth of the epigynal hood. All measures in mm. Values for three species (*S. salsa*, *S. segregata*, *S. aulonia*) were not available and for these species, ratio of length to width was calculated from published figures in Dondale & Redner (1978).

Species	Length	Width	L/W	Hood
<i>S. aulonia</i>			1.4	
<i>S. avida</i>	0.9	0.7	1.3	0.3
<i>S. bilineata</i>	0.5	0.6	0.9	0.1
<i>S. cespitum</i>	0.7	0.7	1.0	0.1
<i>S. chiricahua</i>	0.7	0.6	1.2	0.1
<i>S. communis</i>	0.8	0.7	1.1	0.1
<i>S. crassipalpatum</i>	0.5	0.5	0.9	0.1
<i>S. crassipes</i> (FL)	0.7	0.6	1.2	0.1
<i>S. crassipes</i> (MS)	0.7	0.6	1.3	0.1
<i>S. duplex</i>	0.6	0.6	1.0	0.1
<i>S. floridana</i>	0.6	0.5	1.2	0.1
<i>S. humilis</i>	0.8	0.6	1.3	0.1
<i>S. maxima</i>	0.8	0.7	1.2	0.1
<i>S. mccoocki</i>	0.7	0.7	1.0	0.1
<i>S. mimula</i>	0.8	0.6	1.3	0.1
<i>S. minnesotensis</i>	0.9	0.6	1.7	0.1
<i>S. ocreata</i> (OH)	0.8	0.7	1.1	0.1
<i>S. ocreata</i> (FL)	0.9	0.7	1.3	0.1
<i>S. ocreata</i> (MS)	0.8	0.6	1.3	0.1
<i>S. retrorsa</i>	0.8	0.6	1.3	0.1
<i>S. rovnieri</i>	0.8	0.7	1.1	0.1
<i>S. salsa</i>			1.1	
<i>S. saltatrix</i>	0.7	0.7	1.1	0.1
<i>S. sp. nr. saltatrix</i>	0.6	0.7	1.0	0.1
<i>S. segregata</i>			1.2	
<i>S. stridulans</i>	0.6	0.6	1.1	0.1
<i>S. uetzi</i>	0.8	0.7	1.2	0.1
<i>S. ocr</i> × <i>rov</i> hybrids	0.7	0.6	1.2	0.1
<i>A. georgicola</i>	1.4	1.0	1.4	0.2
<i>G. pulchra</i>	0.9	0.8	1.1	0.2
<i>R. rabida</i>	1.3	1.0	1.3	1.8

in the positions of *S. aulonia* and *S. maxima* Dondale & Redner 1978.

The analysis resulted in three main clades, with *S. minnesotensis* basal to these clades. The largest clade (Fig. 32, Clade A) is comprised of species found in the eastern half of North America; the range of some of the species is limited to the Northeast, some to the Southeast and some ranges extend to the Midwest (see range maps, Dondale & Redner 1978; Stratton 1991, 1997a). Clade A includes 9 of the 11 taxa with tibial bristles (Fig. 34). Nested within Clade A is a clade that includes *S. duplex*, *S. saltatrix* and *S. nr. saltatrix* plus



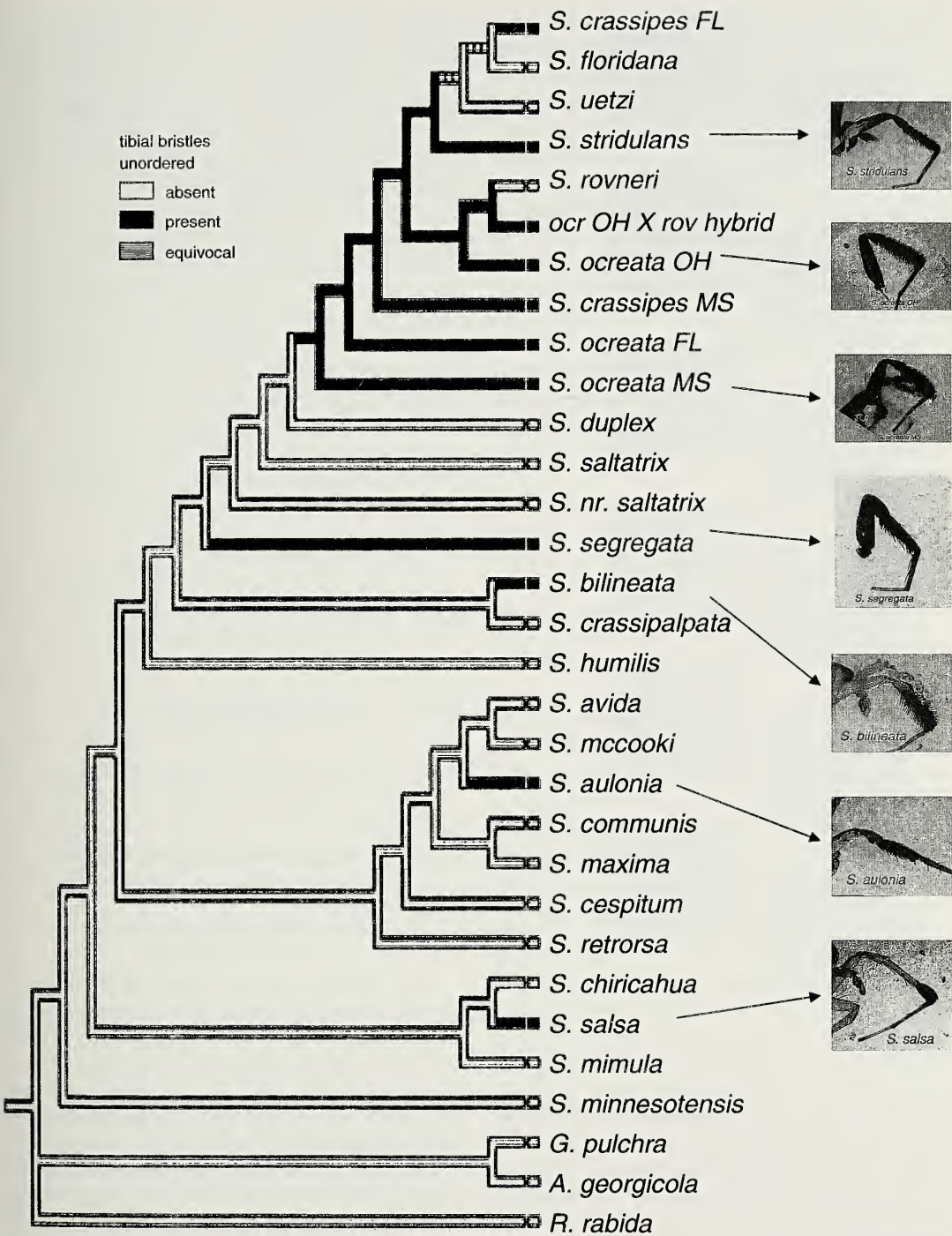


Figure 34.—Mapping of representative tibial bristles, seen in mature males, on the preferred phylogeny.

the *S. ocreata* clade, all defined by a process on the palea of the pedipalp of the male (either a triangular process, Fig. 14, or a finger-like process, Fig. 15) and all found in deciduous woods, or a mix of deciduous and pine forests.

Also within Clade A is a clade that includes *S. bilineata* + *S. crassipalpata*, one of the few clades with significant support from the bootstrap analysis and defined by six characters shared in common.

Also nested within Clade A is the *S. ocreata* clade, which consists of *S. ocreata* (multiple populations), *S. crassipes* (multiple populations), *S. rovneri*, *S. stridulans*, *S. uetzi* and *S. floridana*. The clade is unified by the very distinctive finger-like process on the palea of the male pedipalp (Character 29), sternum color (Character 8), long setae on the ventral surface of the pedipalp (Character 31), and the relative size of the macrosetae (Character 32). Of these characters, only Character 29 is not lost or reversed. Members of this clade have been the most intensively studied with respect to courtship and mating behavior. Two of the taxa in this clade are paraphyletic (*S. ocreata* and *S. crassipes*), suggesting that there are possibly multiple (yet unrecognized) cryptic species.

Clade B includes the widespread eastern *S. avida*, the western *S. mccoocki*, as well as *S. maxima*, *S. aulonia*, *S. cespitum*, *S. communis* and *S. retrorsa*.

The third clade, Clade C include *S. chira-cahua*, *S. mimula* and *S. salsa*. The former two are western, while *S. salsa* is found on the Gulf Coast and Atlantic coast.

**Mapping ornamentation and behavior on preferred phylogenies.**—An examination of the distribution of pigmentation on the first legs of males and bristles on the first pair of legs in males across all taxa in this study suggests that pigmentation may have evolved independently of the bristles, and that both traits can be gained and lost (Figs. 33, 34). For example, pigmentation without bristles is seen in *S. retrorsa*, *S. uetzi* and *R. rabida*, while bristles without pigmentation is seen in *S. bilineata*. When the tibial bristles are mapped onto the preferred phylogeny (Fig. 34) it appears that it evolved independently five or six times with two or three losses in the *S. ocreata* clade. A more detailed comparison of ornamentation on legs of males in the *S. ocreata* clade is presented in Fig. 35. It is clear that in this clade, the full range of pigmentation and bristles occur.

Mapping the major patterns of seismic communication (i.e., drumming vs. stridulation) onto the preferred cladogram shows that the palpal drumming is concentrated in Clade B, while stridulation is prevalent in Clade A (Fig. 36). The *S. ocreata* clade is of particular interest with respect to courtship behavior as within the clade there is the full range of sec-

ondary sexual characters (full tibial bristles, pigment on tibia and or femur, or complete lack of pigmentation or bristles). Within the *S. ocreata* clade, there is a correlation between overt visual signals and the presence of ornamentation. Several species within the clade have reduced or absent pigmentation (*S. rovneri* and *S. uetzi*); these also have reduced visual signals. This study suggests that *S. rovneri*, *S. uetzi* and *S. stridulans* evolved from ancestors that had overt visual signals and these species have subsequently lost visual signals in their courtship. However, as courtship behavior is still unknown for several species with tibial bristles outside of the *S. ocreata* clade (e.g. *S. bilineata*, *S. salsa*, *S. segregata* and *S. aulonia*) strong conclusions concerning the correlation of ornamentation and behaviors throughout the genus is not yet possible.

**Comparison of genital morphology.**—Examination of the pedipalps of these species in light of the hypothesized phylogeny sheds some light on potential homologies of genitalic structures. The most distinctive feature in the male pedipalp of some members of *Schizocosa* is the finger like paleal process (Fig. 16), which is solely found in the *S. ocreata* group. However, the presence of a triangular structure in the same location in the species immediately basal to the *S. ocreata* clade, e.g., *S. saltatrix* (Fig. 13) and *S. duplex* (Fig. 14), suggests that both forms of the paleal process are homologous.

## DISCUSSION

This phylogenetic study confirms that members of Lycosidae are conservative in morphology with large amounts of homoplasy in many characters and low bootstrap support for several branches. The preferred phylogeny presented here (Fig. 32) is a hypothesis of relationships within *Schizocosa* based on a weighting scheme that weights genitalia more heavily than somatic characters and excludes secondary sexual characters. The main clades that are proposed in this study are grouped either by geography (i.e. Clade A) or by a suite of morphological characters (i.e. *S. ocreata* clade, Clade B and Clade C).

This genus is of particular interest for evolutionary biologists because of the relatively large number of species with ornamentation (Figs. 33 & 34). Mapping the tibial bristles on



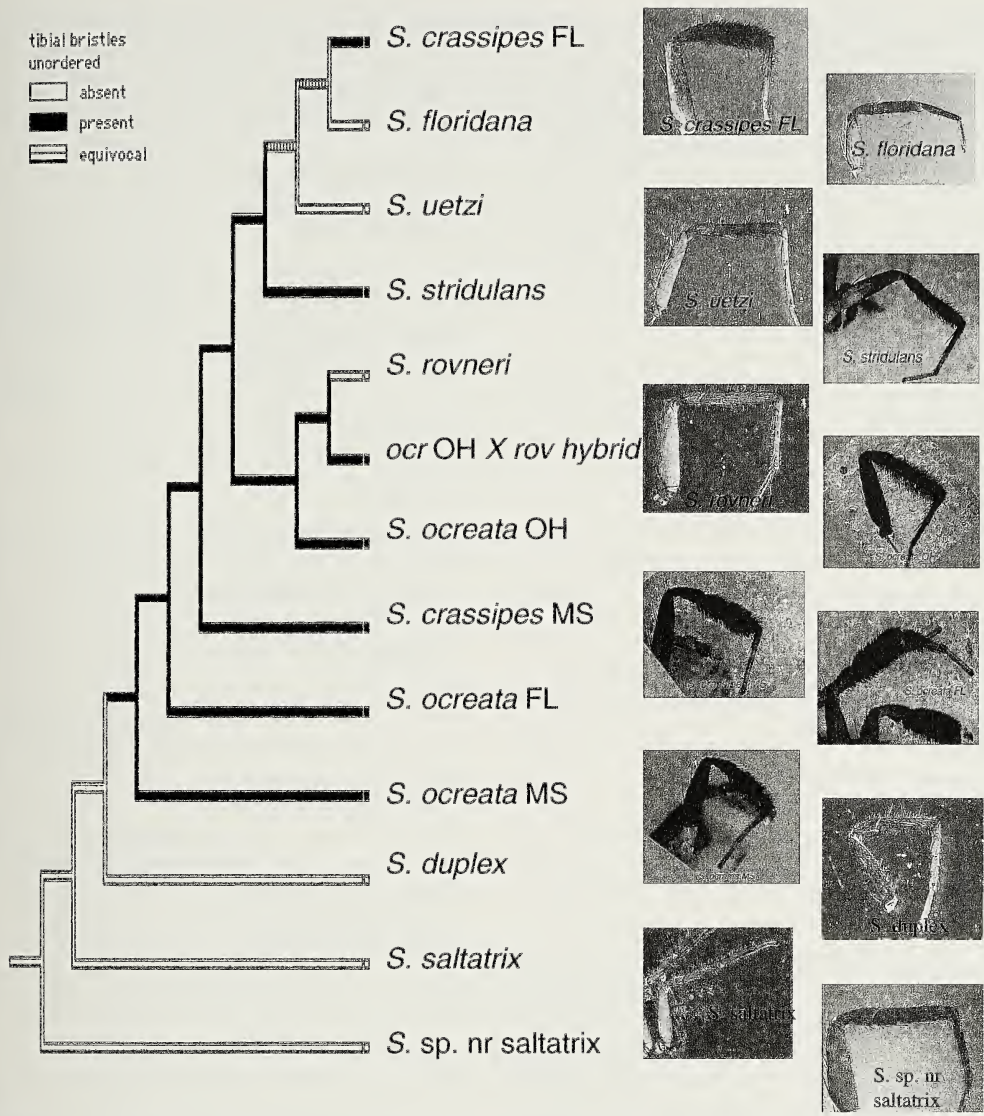


Figure 35.—Cladogram of *S. ocreata* clade + basal species showing presence and extent of bristles on leg I.

the preferred phylogeny shows the distribution (and variation) of the ornamentation. For the tibial bristles, there appears to be five or six independent gains of this character across all of the species in this study, with losses occurring in *S. rovnieri*, *S. uetzi* and *S. floridana*. In Clade A, the character possibly evolved two or three separate times.

While it is challenging to trace the evolution of specific courtship elements, there is clearly a grouping of taxa that show palpal drumming in courtship and a grouping of those that show stridulation in courtship. If the

phylogeny presented in this study is correct, it appears that the species immediately basal to the *S. ocreata* clade (e.g., *S. duplex* and *S. saltatrix*) rely primarily on seismic signals in their courtship. The brush-legged taxa within the *S. ocreata* clade (e.g. populations of both *S. ocreata* and *S. crassipes*) have courtship that involves both seismic signals and visual signals. And, several species within the *S. ocreata* clade have apparently subsequently lost some of the more visual aspects of courtship (e.g., *S. uetzi*, *S. stridulans* and *S. rovnieri*).

Table 5.—Comparison of elements of courtship behavior (both seismic and visual) in species of *Schizocosa*, *Gladicosa* and *Allocosa*.

Species	This study	Previous studies	Not known
<i>S. aulonia</i>			Behavior not known
<i>S. avida</i>		rapid papal drumming, leg 1 arch (Grey & Stratton 1998)	
<i>S. bilineata</i>			Behavior not known
<i>S. cespitum</i>			Behavior not known
<i>S. chiricahua</i>			Behavior not known
<i>S. communis</i>		Palpal drumming (Don-dale & Redner 1978)	
<i>S. crassipalpata</i>	Stridulation		
<i>S. crassipes</i> (FL)		Stridulation, cheliceral strike, leg 1 extend and wave (Miller et al. 1998)	
<i>S. crassipes</i> (MS)		Stridulation, cheliceral strike, leg 1 extend and wave (Miller et al. 1998)	
<i>S. duplex</i>	Stridulation	Stridulation (Hebets & Uetz 2000)	
<i>S. floridana</i>	Stridulation, leg 1 tap		
<i>S. humilis</i>			Behavior not known
<i>S. maxima</i>			Behavior not known
<i>S. mccooki</i>		Papal drumming (Stratton & Lowrie 1984)	
<i>S. mimula</i>			Behavior not known
<i>S. minnesotensis</i>			Behavior not known
<i>S. ocreata</i> (OH)		“Jerky walk” “double tap” (Stratton & Uetz 1983, 1986)	
<i>S. ocreata</i> (FL)	Cheliceral strike double (bilateral arch with legs 1) Stratton, Miller & Miller unpublished data)		
<i>S. ocreata</i> (MS)	Cheliceral strike walk and tap legs 1 (Stratton, Miller & Miller unpublished data)		
<i>S. retrorsa</i>		Palpal drumming, leg 1 wave (Hebets et al. 1996)	
<i>S. rovneri</i>		Series of body bounces (Uetz & Denterlein 1979; Stratton & Uetz 1983, 1986)	
<i>S. salsa</i>			Behavior not known
<i>S. saltatrix</i>	Stridulation, leg 1 arch		
<i>S. sp. nr. saltatrix</i>	Stridulation or body vibration		
<i>S. segregata</i>			Behavior not known
<i>S. stridulans</i>		Stridulation, quick tap of leg 1 (Stratton 1991, 1997a 1997b)	



Table 5.—Continued.

Species	This study	Previous studies	Not known
<i>S. uetzi</i>		Stridulation, leg 1 arch (Stratton 1997b; Hebets 2003)	
<i>S. ocr</i> × <i>rov</i> hybrids		Stridulation, body bounce, double tap, jerky walk (Stratton & Uetz 1986)	
<i>A. georgicola</i>	Stridulation, leg 1 extend and vibrate		
<i>G. pulchra</i>	Stridulation		
<i>R. rabida</i>	Stridulation	Papal scraping, stridulation leg wave (Rovner 1968)	

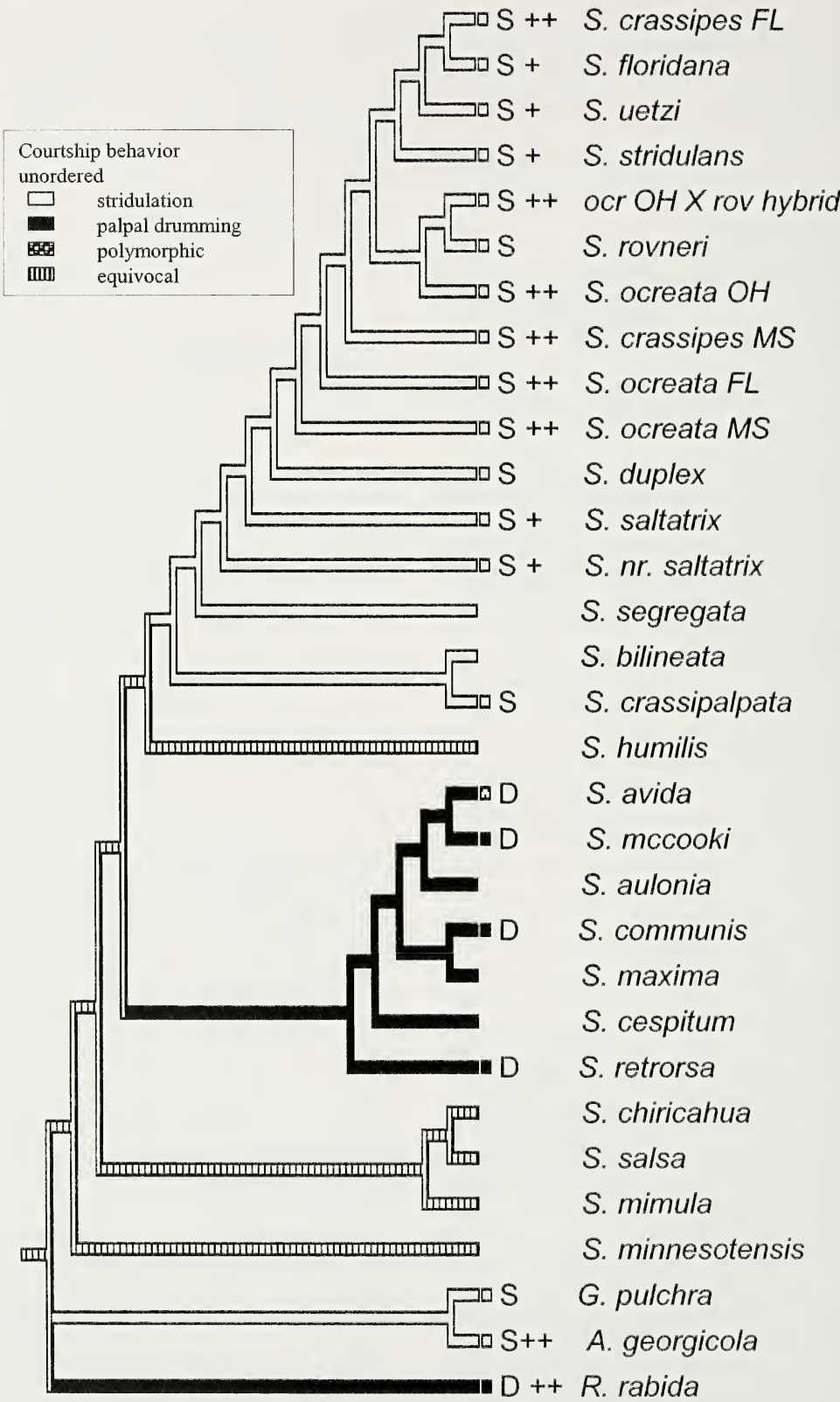
Early work on *S. ocreata* from Ohio and *S. rovneri* suggested that these two species were sibling species (Uetz & Denterlein 1979; Stratton & Uetz 1983, 1986). The subsequent discovery of additional species in the clade (*S. stridulans* and *S. uetzi*) raised questions about the relationship between *S. ocreata* and *S. rovneri*. However, this phylogenetic analysis confirms that these two taxa are each other's closest relatives.

Some currently recognized species within this genus may not reflect phylogenetic lineages as several of the taxa used in this study are paraphyletic (e.g., *S. ocreata*, *S. crassipes* and *S. saltatrix*). The separation of *S. ocreata* (OH) from *S. ocreata* (FL and MS) suggests that these populations are diverging and could be considered separate taxa if a phylogenetic species concept is applied. Miller et al. (1998) showed reduced breeding between crosses composed of *S. ocreata* (OH) and *S. ocreata* (MS, population from Washington Count, Leroy Percy State Park, indicated LP in that study). Likewise, the clear separation of *S. crassipes* (MS) from *S. crassipes* (FL) also suggests divergence. An unpublished study showed reduced interbreeding but a similarity of courtship behavior between both populations of *S. crassipes* (Germano et al. unpublished data). It is intriguing that the *S. ocreata* from Mississippi is basal in the *S. ocreata* clade. The Mississippi River valley has been suggested to be a refuge of deciduous woods during the last ice ages (Delcourt et al. 1980; Delcourt & Delcourt 1987); it is tempting to speculate that perhaps the *S. ocreata* clade diverged from populations along the Mississippi

River valley in the time since the last glaciers. By this scenario, as glaciers retreated in the north, and deciduous woods expanded in the southeast, *S. ocreata* spread first across the southeast and, as populations became isolated they speciated to *S. ocreata* (FL), then *S. crassipes* and the other species within the clade eventually spreading north. The *S. ocreata* clade is now found throughout the eastern U.S.A. with most species found in the southeast. Molecular data could provide an independent test of this hypothesis.

McClintock & Uetz (1996) showed that females of *S. rovneri* preferred *S. rovneri* males that were artificially given tibial bristles. Their preliminary phylogenetic study suggested that *S. rovneri* was basal to *S. ocreata*, thus potentially providing an example of the sensory bias hypothesis or an example where the female preference for a trait (in this case, ornamentation in the form of tibial bristles) preceded the evolution of the trait and provided selection for the trait in subsequent species (in this case *S. ocreata*). However, based on the analyses presented here, *S. rovneri* is derived relative to *S. ocreata* and thus the *S. rovneri* female preference for males with bristles (reported by McClintock & Uetz 1996) is a retained characteristic.

The finger-like process on the palea of the pedipalp seen in the *S. ocreata* clade is unique in wolf spiders. The somewhat similar process seen in *Sosippus* does not appear to be homologous to this structure (Sierwald 2000, fig. 7). High magnification video from the ventral view during copulation confirms that the median apophysis of the male engages the epi-





gynal hood of the female, and the paleal process of the male pinches against the side of the epigynum of the female (Stratton, Miller & Miller, unpub. data). Eberhard (1994) suggested that any time there is physical contact between structures during copulation, the potential exists for that trait to be influenced through female choice during copulation. Thus, this character may give females an additional means to evaluate mates and potentially exercise female choice of gametes. After the examination of thousands of male specimens I have never seen the paleal process broken. It is curious that the clade with a concentration of species with conspicuous secondary sexual characters also has the unique trait of the paleal process that could also be shaped by female choice. It is suggested here that the morphology of primary and secondary genitalic characters in males in this clade may be largely shaped by sexual selection by female choice.

As may be expected due to a lack of informative characters in Lycosinae, the preferred phylogeny did not have strong bootstrap support and a combined morphological and molecular analysis may show better supported results in regard to the phylogenetic relationships of *Schizocosa*.

Indeed, further clarification of this genus and its relatives will provide the phylogenetic context to best interpret behavioral, ecological and evolutionary questions.

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Figure 36.—Distribution of major courtship elements on the preferred phylogeny. The symbol “D” refers to species in which the males are known to show palpal drumming during courtship, “S” refers to species in which males are known to show palpal stridulation. The “+” symbol shows there is arching of leg I, “++” shows species which have extensive visual signals.

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***Schizocosa chiricahua* Dondale & Redner 1978.**—U.S.A.: Arizona: Chochise County, Chiricahua Mts, Southwest Research Station [31°53'N, 109°12'W], 5400', in swimming pool, 15 July 1967 & June 7 1968, V. Roth, 2 ♂ paratypes (AMNH); Arizona: Graham County, near Safford [32°50'N, 109°42'W], 14 July 1956, W. Gertsch & V. Roth, 2 ♂ paratypes, 1 ♀ paratype (AMNH). Published figures: Dondale & Redner (1978, figs. 18, 19, 66–68).

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***Schizocosa crassipes* (Walckenaer 1837).**—U.S.A.: Mississippi: Grenada County, T21N R2E sec. 12, 13N & R3E Sec 7S, 18N [33°44'N, 90°00'W], deciduous woods on hillside, 16 May 1993, G. Stratton, P. Miller, W. Miller, B. Grantham, 1 ♂, 1 ♀ (GES).

***Schizocosa duplex* Chamberlin 1925.**—U.S.A.: Mississippi: Lafayette County, 8 miles SE. of Oxford, T10S R3W Sec 35, 34°36'N, 89°29'W, in pine litter, 18 May 1993, G. Stratton, E. Hebets, 1 ♂, 2 ♀ (GES). Published figures: Dondale & Redner (1978, figs. 6, 42–44).

***Schizocosa floridana* Bryant 1934.**—U.S.A.: Florida: Marion County, Hopkins Prairie, Ocala National Forest [29°10'N, 81°47'W], 25 March 1983, G. Stratton, litter, 4 ♂, 2 ♀ (GES). Published figures: Dondale & Redner (1978, figs. 3, 31–34, 35).

***Schizocosa humilis* (Banks 1892).**—U.S.A.: Pennsylvania: Bucks County, east of Jamieson, Horseshoe Bend, Neshaminy Creek, May 1954, W. Ivie (GES). Published figures: Dondale & Redner (1978, figs. 7, 45, 46).

***Schizocosa maxima* Dondale & Redner 1978.**—U.S.A.: California: Solano County, Fairfield [38°15'N, 122°02'W], April–August 1955, K.W. Haller, 1 ♂ paratype (AMNH); California: Tuolumne County, S. of Highway 108, 5 miles E of

Sonora, elev. 2000', drowned in swimming pool, 14 October 1973, W. Icenogle, 1 ♀ paratype (AMNH). Published figures: Dondale & Redner (1978, figs. 16, 17, 63–65).

***Schizocosa mccooki* (Montgomery 1904).**—U.S.A.: New Mexico: Santa Fe County, Santa Fe [35°31'N, 105°56'W], in pinyon scrub, 17 June 1979, D. Lowrie, 3 ♂, 1 ♀ (GES). Published figures: Dondale & Redner (1978, figs. 13, 15, 59–62).

***Schizocosa mimula* (Gertsch 1934).**—U.S.A.: Colorado: Otero County, Highway 109, 5 June 1967, 1 ♂ (AMNH).

***Schizocosa minnesotensis* (Gertsch 1934).**—U.S.A.: Wyoming: Lincoln County, Kemmerer [41°48'N, 110°32'W], 24 August 1983, R. Parmenter, 2 ♂, 2 ♀ (AMNH).

***Schizocosa ocreata* (Hentz 1844).**—U.S.A.: Ohio: Clermont County, Cincinnati Nature Center [39°07'N, 84°15'W], 6 May 1980, G. Stratton, 1 ♂, 1 ♀ (GES). Published figures: Stratton (1991, figs. 3, 9).

***Schizocosa ocreata* (Hentz 1844).**—U.S.A.: Mississippi: Washington County, Leroy Percy State Park, N. of Highway 12 near entrance of park, T15N R7W, 90°50'W, 33°10'N, 9 April 1993, on knoll by flooded bottomlands, G. Stratton, P. Miller, 1 ♂, 1 ♀ (GES).

***Schizocosa ocreata* (Hentz 1844).**—U.S.A.: Florida: Alachua County, 0.25 miles E. of River Styx on Highway 346 [29°31'17"N, 82°15'47"W], 1 March 1993, G.B. Edwards, P. Cushing, 9 ♂, 3 ♀ (GES).

***Schizocosa retrorsa* (Banks 1911).**—U.S.A.: Mississippi: Lafayette County, 8 miles SE. of Oxford, T10S R3W Sec 35, 34°36'N, 89°29'W, pitfall in pine woods, 28 June–5 July 1993, 1 ♂, 1 ♀, G. Stratton (GES). Published figures: Dondale & Redner (1978, figs. 21, 75–78).

***Schizocosa rovneri* Uetz & Dondale 1979.**—U.S.A.: Kentucky: Boone County, 5 miles W. of Taylorsport, floodplain of Ohio River, "Sandy Run" [39°05'N, 84°41'W], 3 May 1996, K. Delaney, 1 ♂, 1 ♀ (GES). Published figures: Stratton (1991, figs. 2, 7).

***Schizocosa salsa* Barnes 1953.**—U.S.A.: Mississippi: Hancock County, mouth of Jordan River [30°16'N, 89°37'W], on *Juncus* marsh island, 25 June 1993, 1 ♂ (PRM). Published figures: Dondale & Redner (1978, figs. 24, 79, 80).

***Schizocosa saltatrix* (Hentz 1844).**—U.S.A.: Mississippi: Lafayette County, 8 miles SE. of Oxford, T10S R3W Sec 35, 34°36'N, 89°29'W, "Lonesome 80," pine deciduous woods, 16 March 1996, G. Stratton & P. Miller, 1 ♂, 1 ♀ (GES). Published figures: Dondale & Redner (1978, figs. 4, 39–41).

***Schizocosa* sp. nr *saltatrix*.**—U.S.A.: Mississippi: Wilkinson County, 5 miles E of Doloroso on Smith Rd, S. of Homochito River, 31°20'N,

92°45'W, uplands deciduous forest, 10 April 1993, G. E. Stratton, P.R. Miller, 1 ♂, 1 ♀ (GES).

***Schizocosa segregata* Gertsch & Wallace 1937.**—U.S.A.: *Florida*: Levy County, 28 April 1934, # 298, H.K. Wallace, 1 ♂, 1 ♀, paratypes (poor condition); *Texas*: Edinburg [26°18'N, 98°10'W], 1934, S. Mulaik, 1 ♂ (poor condition) (AMNH). Published figures: Dondale & Redner (1978, figs. 23, 81, 82).

***Schizocosa stridulans* Stratton 1984.**—U.S.A.: *Illinois*: Mason County, Sand Ridge State Forest [40°24'N, 89°52'W], 7 June 1985, G. Stratton, L. Hartz, 1 ♂, 1 ♀ (GES). Published figures: Stratton (1991, figs. 1, 5, 6, 13).

***Schizocosa uetzi* Stratton 1997.**—U.S.A.: *Mississippi*: Lafayette County, 8 miles SE of Oxford, T10S R3W Sec 35, 34°36'N, 89°29'W, "Lonesome 80," mixed pine and hardwoods, 4 July 1992, G. Stratton, 1 ♂, 1 ♀ (GES). Published figures: Stratton (1997, figs. 1–5).

***Schizocosa ocreata* × *Schizocosa rovneri* hybrids.**—Cross between *S. ocreata* ♀ from Ohio and *S. rovneri* ♂ from Kentucky, 1980–1982, 1 ♂ (GES). Cross between *S. rovneri* ♂ from Kentucky

and *S. ocreata* ♀ from Ohio, 1980–1982, 1 ♀ (GES).

***Allocosa georgicola* (Walckenaer 1837).**—U.S.A.: *Mississippi*: Lafayette County, 8 miles SE of Oxford, T10S R3W Sec 35, 34°36'N, 89°29'W, "Lonesome 80," pitfall in mixed pine and hardwoods, 16–24 September 1992, G. Stratton, P. Miller, 1 ♂, 1 ♀ (GES). Published figures: Chamberlin & Ivie (1944, fig. 57). Pedipalps and epigyna of the closely related *H. helluo* (Walckenaer 1837) are figured in Kaston (1948, figs. 1065, 1066, 1090, 1105) and Dondale & Redner (1990, figs. 43–47).

***Gladicosa pulchra* (Keyserling 1877).**—U.S.A.: *Tennessee*: Hardeman County, Chickasaw State Park [35°22'N, 88°50'W], pine deciduous woods, 1 November 1992, G. Stratton, 1 ♂, 1 ♀ (GES). Published figures: Brady (1986, figs. 3, 10–14, 39–42).

***Rabidosa rabida* (Walckenaer 1837).**—U.S.A.: *Mississippi*: Lafayette County, 8 miles SE of Oxford, T10S R3W Sec 35, 34°36'N, 89°29'W, pine deciduous mixed, 5 August 1991, G. Stratton, P. Miller, G. Miller, 1 ♂, 1 ♀ (GES). Published figures: Brady & McKinley (1994, figs. 1, 6, 11–14) and Kaston (1948, figs. 1077, 1079, 2006).



## FACTORS AFFECTING CANNIBALISM AMONG NEWLY HATCHED WOLF SPIDERS (LYCOSIDAE, *PARDOSA AMENTATA*)

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**ABSTRACT.** Cannibalism is a common phenomenon among young wolf spiders (Lycosidae). The purpose of this study was to investigate how various factors influence cannibalistic tendencies in hatchlings of *Pardosa amentata* (Clerk 1757). The basic experimental approach was to place pairs of unfed hatchlings of similar body mass in small containers without prey and to measure if and when cannibalism happened. From the data, we identified three different cannibalistic strategies. One large group of hatchlings never cannibalized and thus died from starvation. Another group cannibalized shortly before the time at which they were predicted to die from starvation. In these spiders, there was a strong positive relationship between average body mass of the contestants and their latency to cannibalize. A third group cannibalized quickly and the latency to cannibalize in these spiders was independent of body mass. We also tested if cannibalistic tendencies were higher among unrelated pairs than among pairs of siblings, but we did not find any support for this hypothesis. In another experiment we tested if maternal effects influenced cannibalism, i.e. if siblings from certain mothers were more cannibalistic than siblings from others. We did not find any evidence that maternal effects influenced whether or not cannibalism occurred. However, when cannibalism did occur, the latency to cannibalize varied significantly among siblings from different mothers beyond what would have been predicted solely from hatchling body mass.

**Keywords:** Lycosidae, intraspecific predation, spiderlings, kin recognition, maternal effects

Cannibalism among wolf spiders is often observed in the field. One example is *Pardosa lugubris* (Walckenaer 1802) which seems to be the most important predator of its own species (Edgar 1969), and it was estimated that juveniles of this species included conspecifics as 29% of their total diet (Hallander 1970). Other examples are *Schizocosa ocreata* (Hentz 1844) and *Pardosa milvina* (Hentz 1844) in which cannibalism is assumed to be an important regulating factor on population density (Wagner & Wise 1996; Buddle et al. 2003).

A variety of factors has been suggested as potential selective forces, promoting or inhibiting cannibalistic behavior. The most obvious advantage connected with cannibalism is that the cannibal gains a meal in addition to the normal diet and cannibals often show higher growth and survival rates than their non-cannibalistic conspecifics (Polis 1981). As can-

nibals are facing prey with similar predatory abilities, an obvious cost of cannibalism is the risk of retaliation. Another intriguing cost of cannibalism is the potential loss of inclusive fitness when a cannibal kills a genetically related individual (Elgar & Crespi 1992; Pfennig & Sherman 1995). If this cost is large, we would predict spiders to be able to distinguish between kin and non-kin and to treat kin and non-kin differently (Pfennig & Sherman 1995). Kin recognition has been shown to occur in many cannibalistic animals (see references in Pfennig 1997) and also some spiders seem to be able to identify and subsequently avoid eating a close relative (Evans 1999; Bilde & Lubin 2001; Anthony 2003; Roberts et al. 2003). Wolf spider females carry their young on the abdomen for about a week. Thus, hatchlings have a good opportunity to learn chemical or visual cues, which could later be used to recognize siblings from non-siblings.

Adult wolf spiders can survive starvation

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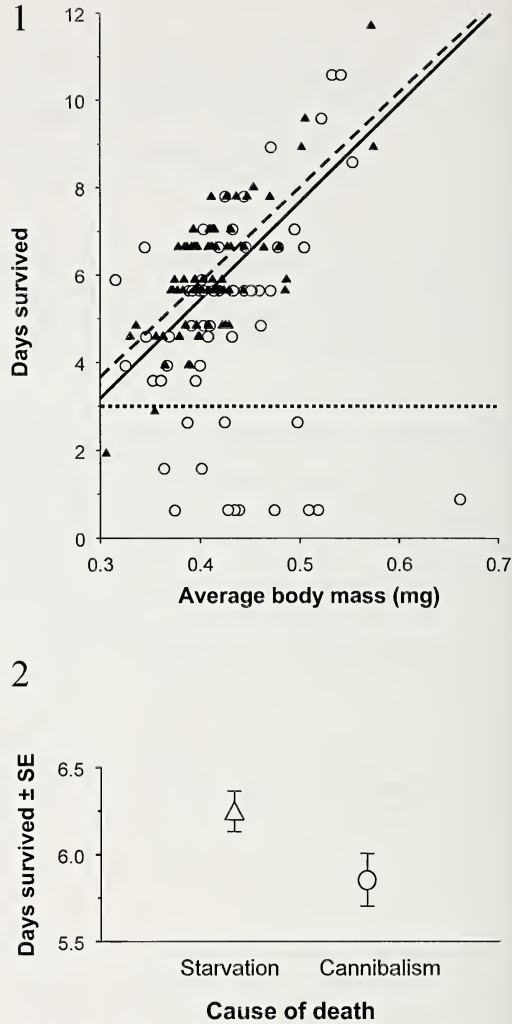
for several months (Anderson 1974). Newly hatched spiderlings on the other hand can only survive a few days or weeks before their nutrient reserves are depleted (Wagner & Wise 1996; Toft & Wise 1999). This means that the first meal is of utmost importance for spiderlings and cannibalism can therefore be important for juvenile survival.

In the present experiments we investigated cannibalistic tendencies among equally sized pairs of unfed hatchlings and provided them no choice other than to cannibalize or to die from starvation. Using this approach we evaluated different hypotheses about what influences cannibalistic tendencies in the hatchlings. In the first experiment, we paired sibling and non-sibling hatchlings in order to test if cannibalism was dependent on kinship. From these results we also describe three apparently different strategies among hatchlings. Potentially, a mother of a brood can affect the condition of her spiderlings and thus also their cannibalistic propensities, for example through her nutritional status before reproduction. The rates of cannibalism may also vary between closely related species or among and even within populations, due to genetic differences (Thibault 1974; Stevens & Mertz 1985; Tarpley et al. 1993). In a second experiment we therefore tested if there was variation in cannibalistic tendencies among hatchlings descending from different mothers.

METHODS

**The wolf spider.**—The wolf spider *Paradosa amentata* is abundant in Europe in many open, humid habitats, especially grasslands and agricultural fields with a well-developed litter layer (Alderweireldt & Maelfait 1988). Reproduction takes place in May–July. Females carry the eggsac for 2–3 weeks and hatchlings spend about one week on their mother’s abdomen before they disperse (Roberts 1995).

**Experiment 1.**—The purpose of this experiment was to test if kinship affected cannibalism and to describe the cannibalistic tendency of hatchlings in general. Subadult male and female *P. amentata* spiders were collected in spring in a meadow at Stjær, Denmark (56°07’N, 9°91’E), and brought to the laboratory. They were housed individually in plastic containers (diameter 35 mm, height 80 mm) with a plaster bottom, which was wetted



Figures 1–2.—1. Effects of body mass and cause of death on the survival time of wolf spider hatchlings (Experiment 1). Survival time was measured from the time spiderlings were paired. Each point represents the time passed until one of the two spiders in a pair died from starvation (black triangles) or from cannibalism (open circles). Body mass is the average mass of the two hatchlings in a pair. Regression lines are based on spiders that died after day 3, i.e. > 7 days old (above horizontal dotted line); death from starvation = broken regression line, cannibalism = solid regression line. 2. Number of days survived adjusted for average body mass (least squares means, calculated on spiders dying after day 3 in the experiment, i.e. > 7 days old).

frequently to maintain a permanent high humidity in the container. The spiders were fed wild type *Drosophila melanogaster* (Meigen) in excess until maturity. Fruit flies were raised



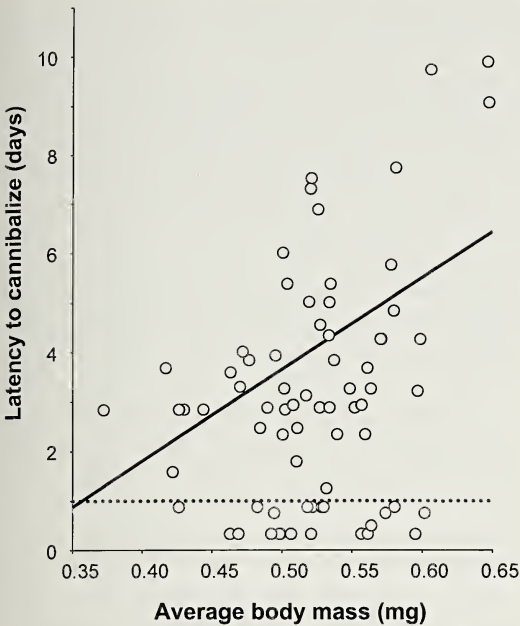


Figure 3.—Relationship between average body mass of hatchling pairs and their latency to cannibalize (Experiment 2). The two spiderlings always originated from the same eggsac. Each point represents the time passed until cannibalism occurred. The regression line is based on spiders cannibalizing after day 1 (above horizontal dotted line), i.e. > 7 days old. About 64% of the spiders did not cannibalize at all and are not shown in the figure.

on instant *Drosophila* medium (formula 4–24 Plain, Carolina Biological Supply, Burlington NC), mixed with crushed dogfood (Techni-Cal ADULT®, Martin Pet Foods, Canada). Fully matured females were mated with a single male and different males were used for each female in order to avoid offspring from different females being half-siblings. The young descending from eight eggsacs were chosen for the experiment. These eggsacs hatched within a period of four days and when hatchlings were  $4 \pm 1$  days old, they were weighed to the nearest  $\mu\text{g}$ . Pairs of hatchlings descending from the same eggsac ( $n = 71$ ) or from different eggsacs ( $n = 71$ ) were then placed in the same plastic tube (diameter 20 mm, height 60 mm). The tubes contained a plaster bottom, which was wetted frequently to maintain a permanent high humidity in the container. Body mass asymmetry was avoided by pairing spiders of almost equal body mass (mean body mass  $\pm$  SE =  $421 \pm 4 \mu\text{g}$ ; mean weight difference  $\pm$  SE =  $2.6 \pm 0.2 \mu\text{g}$ ; max.

weight difference =  $14 \mu\text{g}$ ). Spiderling age (days since hatching) at the start of the experiment varied up to three days within a pair. Experimental conditions were set at  $25 \pm 0.1^\circ\text{C}$ ; 16L:8D. The spiderlings never received any food but had constant access to water from the plaster. Spiders were checked for deaths twice daily. Cannibalism left clear marks of partly or fully digested body parts and a stereomicroscope was used in case of doubt. An outcome of the experiment was recorded when one of the two hatchlings was dead, due to starvation or cannibalism.

**Experiment 2.**—The purpose of this experiment was to test if the tendency to cannibalize varied among spiderlings from different eggsacs. Females of *P. amentata* with an eggsac were collected from the same location as in experiment 1, thus, we were only able to test for maternal effects on cannibalism and not for paternal effects. The spiders were taken to the laboratory and kept as in experiment 1. At 4 days of age, hatchlings from 19 eggsacs were weighed. At day 6, hatchlings of approximately the same body mass were paired (mean body mass  $\pm$  SE =  $519 \pm 3 \mu\text{g}$ ; mean weight difference  $\pm$  SE =  $2.7 \pm 0.2 \mu\text{g}$ ; max. weight difference =  $13 \mu\text{g}$ ). In all pairs, the two hatchlings descended from the same eggsac ( $n = 205$  pairs, 4–17 pairs from each eggsac). Experimental conditions and procedures were the same as in experiment 1.

**Data analysis.**—Differences in the cause of death between kin and non-kin hatchling pairs were analyzed using the Pearson statistic. The latency to cannibalize between kin and non-kin were analyzed using Student's t-test, after testing for equal variances (Bartlett's Test,  $\alpha > 0.05$ ). Linear regression was used to test for correlation between mean body mass of pairs and the time spent before one of the two hatchlings died from either cannibalism or starvation. Regression lines were analyzed using Analysis of Covariance (ANCOVA), with body mass as the covariate. First, we tested for equal slopes and if they were not significantly different, we tested if intercepts were equal and calculated means adjusted for the covariate (least squares means). We used logistic regression to test if hatchlings from different eggsacs differed in their probability to cannibalize or to die from starvation. All statistical analyses were performed with JMP 5.0 for Windows (SAS Institute).

## RESULTS

**Experiment 1.**—The proportion of pairs resulting in a cannibalistic event was not affected by kinship, i.e. whether or not the two spiders in a pair originated from the same eggsac (Pearson  $\chi^2 = 0.26$ ,  $P = 0.61$ ; siblings 41 %, non-siblings 45 %,  $n = 142$ ). Furthermore, the time passing until a cannibalistic act occurred did not differ between sibling and non-sibling pairs (t-test,  $DF = 59$ ,  $P > 0.80$ ; siblings =  $8.82 \pm 0.40$  days  $\pm$  SE, non-siblings =  $8.99 \pm 0.49$  days  $\pm$  SE). Thus, we found no evidence that relatedness affected the cannibalistic tendency in hatchlings. In our description of general patterns of cannibalism below, we therefore pool data from siblings and non-siblings.

Fig. 1 shows the relationship between average body weight of hatchling pairs and the time until one of the two hatchlings died. The data indicate a presence of three different cannibalistic strategies. One group of hatchlings never cannibalized (57%) and consequently died from other reasons than cannibalism. In this non-cannibalistic group, there was a positive correlation between mean body mass and survival time of the first dying hatchling (linear regression,  $t = 8.45$ ,  $n = 79$ ,  $P < 0.0001$ ;  $R^2 = 0.48$ ). A similar type of positive correlation was found in pairs where cannibalism happened after 3 days of the experiment (33% of all pairs; linear regression,  $t = 6.95$ ,  $n = 47$ ,  $P < 0.0001$ ;  $R^2 = 0.52$ ). The regression line of spiders cannibalizing after day 3 of the experiment (i.e.  $> 7$  days old) and the regression line of spiders dying from other reasons than cannibalism did not have significantly different slopes (ANCOVA,  $SS = 0.04$ ,  $F = 0.03$ ,  $P = 0.85$ , Fig. 1), but the intercepts of the two regression lines differed significantly (ANCOVA,  $SS = 4.53$ ,  $F = 4.20$ ,  $P = 0.04$ ). The least squares means of survival days adjusted for body mass showed that spiders cannibalizing after day 3 ( $> 7$  days old), did so on average 0.4 days (i.e. less than 10 h) before equal sized spiders would die from other reasons than cannibalism (Fig. 2). Besides the two strategies where spiders either died or cannibalized in a size dependent way, 10% of the pairs cannibalized early, within the first 3 days of the experiment. Among these pairs, there was no correlation between mean body mass and the time passing until cannibalism

occurred (linear regression,  $t = 0.93$ ,  $n = 14$ ,  $P = 0.37$ ,  $R^2 = 0.07$ ).

**Experiment 2.**—We found the same three cannibalistic patterns in this experiment as described from experiment 1 (Fig. 3). Either spiders did not cannibalize at all (64.4%); they cannibalized in a body mass dependent way (25.4%, linear regression,  $n = 52$ ,  $t = 4.57$ ,  $P < 0.0001$ ,  $R^2 = 0.29$ ); or they cannibalized within the first day of the experiment (i.e. before being 7 days old) regardless of body mass (10.2%, linear regression,  $n = 21$ ,  $t = 0.18$ ,  $P = 0.86$ ,  $R^2 = 0.002$ ).

Mother identity did not affect whether or not cannibalism occurred within a pair of hatchlings (logistic regression, Wald  $\chi^2 = 23.05$ ,  $DF = 18$ ,  $P = 0.19$ ). However, when cannibalism did occur, the latency to do so varied significantly among hatchlings from different eggsacs, after correcting for the effect of body mass (ANCOVA on the latency to cannibalize with mean body mass as covariate,  $DF = 13$ ,  $SS = 186.5$ ,  $F = 5.20$ ,  $P < 0.0001$ , Fig. 4); five eggsacs in which fewer than three pairs cannibalized were omitted from this analysis, thus, 14 eggsacs were included with a total of 65 pairs.

## DISCUSSION

The results of this study indicate that three different cannibalistic strategies exist in the wolf spider hatchlings. Either we observed no cannibalism, late and size dependent cannibalism, or early and size-independent cannibalism. This pattern appeared in two separate experiments, which suggests that it is a general pattern of this wolf spider species.

More than half of the spiderlings belonged to the group that never cannibalized and consequently died from other causes than cannibalism. As all spiderlings were deprived of food we expect that the main part of these non-cannibalizing spiders died from starvation. The body mass of an animal probably correlates positively with the amount of nutrient reserves that are stored in the body. Furthermore, light animals are often found to have proportionally higher specific metabolic rate than heavier animals (Edwards 1946; Phillipson 1963). Together, these two factors may explain the observed pattern of lighter spiders dying from starvation sooner than heavier spiders.

The spiders that did cannibalize could be



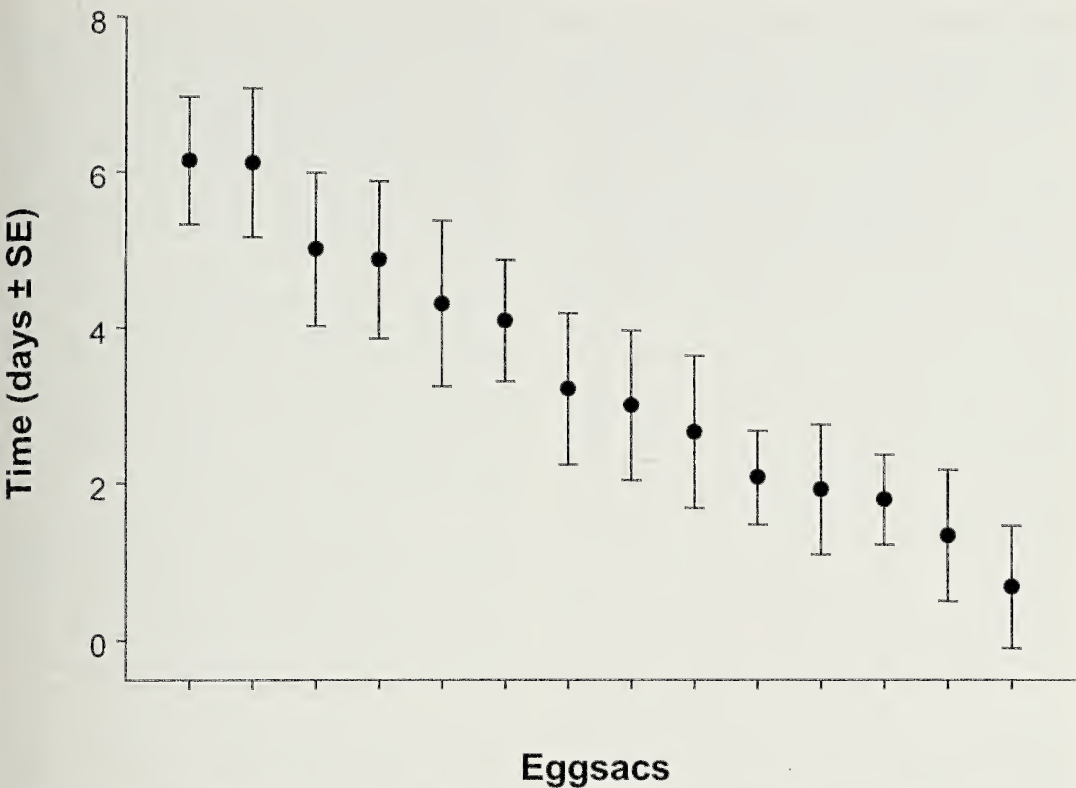


Figure 4.—Effect of eggsac origin on the latency to cannibalize in pairs of equal sized siblings (Experiment 2). Points show the time passing until cannibalism occurred adjusted for the effect of body mass ( $n = 3\text{--}9$  pairs of siblings per eggsac, five eggsacs were not included because less than 3 pairs of spiderlings from these eggsacs cannibalized).

divided in two groups: a group where the onset of cannibalism was dependent on body mass, and a group, which cannibalized early. In the body mass dependent cannibalism lighter pairs cannibalized earlier than heavier pairs, which suggests that the latency to cannibalize depended on their level of nutrient reserves. In fact, this group of spiderlings generally waited to cannibalize almost until the time when they were predicted to die from starvation, which suggests that they chose to cannibalize as a very last option. In a relatively small proportion of spider pairs (ca. 10%) cannibalism appeared early in the experiment regardless of their body mass. This group of spiders did not seem to be under severe food stress when the cannibalism occurred, suggesting that these spiders had a higher keenness to cannibalize. Different cannibalistic strategies among individuals within a species have also been observed in other animals. In salamanders (Lannoo et al. 1989)

and spadefoot toad tadpoles (Pfennig et al. 1993) individuals can be divided into cannibalistic and non-cannibalistic forms and cannibalistic individuals are often characterized by actual morphological and physiological differences that enhance this feeding strategy. Field studies have shown that conspecifics comprise a large part of the diet in juvenile and adult wolf spiders (Edgar 1969; Hallander 1970). However, in this experiment spiderlings were rather reluctant to cannibalize, even though they were kept in the same container with no escape possibilities. Why did the majority of hatchlings refuse to cannibalize when the consequence of such a decision is death from starvation? Our experimental setup does not provide a clear answer to that question. One likely explanation is that they fear the cost of retaliation. The risk associated with attacking decreases as the asymmetry in body mass/size increases. Samu et al. (1999) found that the body mass

ratio between two juvenile spiders was the most important factor influencing cannibalism, and cannibalism was not observed within 24 hours if the body mass ratio was less than 2:1 (predator:prey). Here we paired spiderlings of equal body mass, which in principle have similar predatory abilities and therefore provide roughly 50/50 chance of dying, unless there are different risks associated with being an attacker or a defender. The fact that a large proportion of the spiders postponed cannibalism almost until they died from starvation indicates that risk of retaliation or other factors inhibit cannibalism. It is possible that cannibalism occurred when the risk of dying from starvation had outweighed these risks. We cannot exclude the possibility that some of the cannibalistic events happened after one of the spiders was dead or almost dead from starvation. If so, then cannibalistic acts should only confer little or no risk of retaliation. Another potential cost of cannibalism is the risk of receiving pathogens from conspecific prey (Pfennig et al. 1998). If this is a real cost in the field, it would explain the general reluctance to cannibalize in the majority of the spiders. However, we are not aware of any pathogens that might cause such a risk in wolf spiders, especially not among young hatchlings.

A general inhibition of cannibalism can be an indirect method to avoid eating relatives. Where such an inhibition has been demonstrated, it is often expressed in certain life stages. Filial cannibalism, for example, is inhibited in reproductively active females of the wolf spider *Scizocosa ocreata* (Wagner 1995). Moreover, cannibalism was less frequent in the 2nd instar of the wolf spider *Hogna helluo* (Walckenaer 1837), compared to 3rd instar spiderlings (Roberts et al. 2003). Avoidance of related prey can also be direct through kin recognition where relatives are recognized and disregarded as prey (Pfennig 1997). There is one study that supports kin discrimination among young spiderlings in a wolf spider (Roberts et al. 2003). In this species a higher frequency of cannibalism was observed in pairs of non-siblings compared to pairs of siblings. In the present experiment, we did not find any evidence supporting the hypothesis that siblings cannibalized each other less frequently than non-siblings. Thus, either *Pardosa amentata* hatchlings cannot recognize a

sibling from a non-sibling, or they do not care and cannibalize nevertheless. These results are also in contrast to data on social (*Diaea ergandros* Evans 1995) and sub-social (*Stegodyphus lineatus* Latreille 1817) spiders (Evans 1999; Bilde & Lubin 2001), in which the studies showed kin recognition and kin discriminating cannibalistic behavior. Compared to solitary spiders, social spiders and sub-social spiderlings spend long periods of time close to relatives and it is possible that such frequent encounters with relatives are a requirement for the evolution of kin recognition (Bilde & Lubin 2001). Spiderlings of a clutch do not leave their mother's abdomen at the same time but dispersal is distributed over several days and over a relatively large area (D. Mayntz, pers. obs.). Thus, the only time wolf spiders have a high chance of meeting siblings is when the spiderlings are gathered on their mother's abdomen. Avoiding cannibalism of kin may possibly be accomplished during other routes than actual kin recognition. For example, intra-brood cannibalism in *Pardosa pseudoannulata* (Bösenberg & Strand, 1906) rarely occurred due to the small size difference within the brood (Iida 2003). Moreover, *P. pseudoannulata* did not seem to cannibalize siblings less frequently than non-siblings (i.e. no evidence for kin recognition).

When we tested for variation in cannibalistic tendencies among hatchlings from different eggsacs, we did not find any evidence that maternal effects influenced whether or not cannibalism happened. However, when cannibalism did occur, hatchlings from different eggsacs showed variable latencies to do so (Fig. 4). We collected the eggsacs in the field. This made it impossible for us to assess the genetic influence from the fathers, and prevented us from separating genetic effects from other maternal effects that might have affected the hatchlings' tendency to cannibalize. Beyond pure genetic factors, possible maternal factors affecting cannibalistic tendency may include the nutritional history of the mother, the age of mother, or size of the brood. Heritability of cannibalistic behavior has been shown in fish, flour beetles, corn borers and ladybird beetles (Thibault 1974; Stevens & Mertz 1985; Tarpley et al. 1993; Wagner et al. 1999) but so far not in spiders. Half-sib experiments or actual selection experiments are needed before we can clarify how much ge-



netic effects contribute to the observed variation in the latency to cannibalize.

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## DATA ON THE BIOLOGY OF *ALOPECOSA PSAMMOPHILA* BUCHAR 2001 (ARANEAE, LYCOSIDAE)

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**ABSTRACT.** This paper presents electron micrographs of the genitalia of *Alopecosa psammophila*, describes the morphological characteristics of the species and also gives information on its habitat preference, the co-occurring ground-dwelling spiders, and the phenological characteristics of the species. Barber pitfall trappings have been carried out since 2000 in dry sandy grasslands in three regions of Hungary: the Kiskunság area (Kiskunság National Park); the Nyírség area (Hortobágy National Park); and since 2004 the Kisalföld area (Fertő-Hanság National Park). Specimens of the species, hitherto unknown in Hungary, have been collected from 17 localities in all three areas. We collected specimens in calciferous open sand steppes and in acidic open sand steppes. In the females, two activity periods were apparent (from April to end July and in October). A few males were collected in April and in October–November they had an extreme activity peak. We assume that the species has adult specimens throughout the winter. *Alopecosa psammophila* is most similar to *Xysticus ninni* Thorell, 1872 and *Zelotes longipes* (L. Koch 1866) in terms of its environmental needs.

**Keywords:** Wolf spider, sandy grasslands, palpal organ, phenology, habitat preference

The species *Alopecosa psammophila* Buchar 2001 is known only from warm and dry sandy habitats of southern Moravia and from southern Slovakia (Buchar 2001). On the basis of the habitat characteristics of the holotype, and because they were found so close to Hungary, it was highly likely that the species would occur in Hungary, as dry sandy grasslands occur in large areas in the Carpathian Basin.

The ultimate goal of the investigations into Hungarian sandy grasslands was to explore the biology of the species in precise details. We wished to focus primarily on the phenological characteristics, the habitat preference and the co-occurring spiders. In addition we also wished to publish pictures of the genitalia of the Hungarian specimens taken using a scanning electron microscope, as only drawings of the species have hitherto been known in the international literature (Buchar 2001).

### METHODS

Barber pitfall trappings have been carried out in nine sandy grasslands in the Kiskunság area (Kiskunság National Park—coordinates

of the central site of the study area (Fülöpháza) Lat. 19°24' N, Long. 46°52' E) and eight sandy grasslands in the Nyírség area (Hortobágy National Park—coordinates of the central site of the study area (Bátorliget) Lat. 47°42' N, Long. 17°47' E) since 2000 as part of the project “Monitoring grasslands,” itself part of the national program Biodiversity Monitoring. The appropriate processing of the specimens collected in 2000 in the 170 ground traps, operated throughout the entire vegetation season with 10 traps in each of the 17 habitats, provided us with an ample opportunity to examine the occurrence of *Alopecosa psammophila*.

In addition to the two large regions under investigation since 2000, we commenced similar investigations in the sandy grasslands of the Small Hungarian Plain (Kisalföld, part of the Fertő-Hanság National Park—coordinates of the central site of the study area (Gönyű) Lat. 47°40' N, Long. 20°14' E), which lies in the northwestern part of the country. Figure 1 of Central Europe shows the type locality of the species, its habitat in Slovakia (Buchar 2001), as well as the sampling sites in Hungary.





Figure 1.—The occurrence of the *Alopecosa psammophila* in Central Europe. ■ = the type locality; ▲ = sampling site in Slovakia; ● = sampling sites in Hungary. 1● = Kiskunság National Park: 9 different study sites; 2● = Nyírség region: 8 different study sites; 3● = Small Hungarian Plain (Kisalföld).

In the Kiskunság area we also paid close attention to the characteristics of the habitats. This way we had the opportunity to explore the relationship between the abundance of *A. psammophila* and the environmental variables including size of the habitat investigated, average open sand surface, average coverage of lichens and mosses, average coverage of the sand and mosses, average coverage of the leaf-litter, average coverage of vegetation, average vegetation height. We used multiple regression models to evaluate the effects of the seven variables on the number of individuals (Barta et al. 2000). For investigating which species have the closest habitat association with *Alopecosa psammophila* we used hierarchical cluster analysis (Tóthmérész 1993). The electron micrographs were made in the Hungarian Natural History Museum, Budapest (dr. Krisztina Buczkó) with a HITACHI SN 2600 scanning electron microscope. The voucher specimens are deposited in the collection of HNHM.

RESULTS

**Morphology.**—Figs. 2–5 show electron micrographs of the genitalia of the Hungarian specimens. In both male and female genitalia



Figures 2–5.—Genitalia of *Alopecosa psammophila*. 2. Left male palp, ventral view.



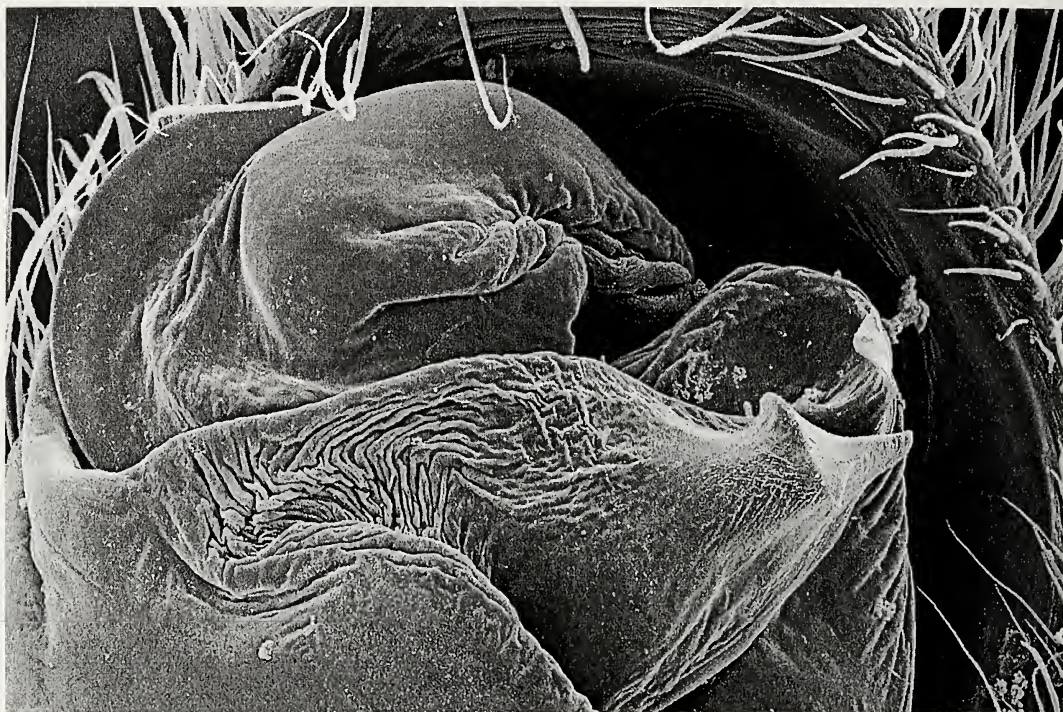


Figure 3.—Tegular apophysis and apical division.

the three-dimensional structure of the organs carries the specific information that allows the recognition of the species. In the male palp the spear shape of the tegular apophysis can be understood by mentally combining the ventral (Fig. 2–3.) and retrolateral (Fig. 4) views.

**Occurrence in Hungary.**—This species, hitherto unknown to Hungary, has been collected from 17 different habitats (sampling sites) in the three different areas. The 17 habitats examined yielded specimens of the species from 12 and 11 locations in 2001 and 2002, respectively. The species occurred in 16 out of the 17 Hungarian sandy grasslands investigated. Add to this the sandy grasslands in the Kisalföld area which also yielded specimens of the species.

**Phenology.**—In the collection period between the beginning of April and the beginning of November 2001 (the longest collection period within one calendar year), 46 females and 54 males were collected. In the case of the females, two activity periods were evident. The first period lasted from April to the end of July, culminating in the second half of May (Fig. 6). The peak coincided with the collection dates published by Buchar (2001).

We also collected males in April, which also coincided with Buchar's (2001) observations. In summer and early autumn periods there were no males in the samples, but in the second half of October and in November there was an extreme activity peak of males. We assume that the species has adult specimens throughout the winter. The November (2004) trappings also yielded males at Gönyű (Small Hungarian Plain).

**Habitat preference.**—We collected the specimens in the calciferous open sand steppes (*Festucetum vaginatae danubiale*) in the area between the rivers Danube and Tisza and on the Small Hungarian Plain, and in the acidic open sand steppes of the Nyírség area (*Festuco vaginatae-Corynephorretum*). We can conclude that the species is generally widespread in the ground-dwelling fauna of any dry sandy grassland in the Carpathian Basin. However, we were unable to find any significant relationships between its presence/absence or its relative abundance and the measured characteristics of the flora of the grasslands investigated (non-significant effects of all seven variables), apart from it being a very strong indicator of sand.





Figure 4.—Same as Fig. 3, retrolateral view.

**Spider communities.**—Sandy grasslands seem to have rather similar spider communities all over Hungary. These communities were characterised by specialist psammophilous species and were basically unaffected by wide regional separation and/or sand type. The dominant species at the study sites included *Alopecosa cuneata* (Clerck, 1757); *Alopecosa cursor* (Hahn, 1831); *Alopecosa sulzeri* (Pavesi, 1873); *Berlandina cinerea* (Menge, 1872); *Callilepis nocturna* (Linnae-

us, 1758); *Gnaphosa mongolica* Simon, 1895; *Thanatus arenarius* Thorell, 1872; *Thanatus pictus* L. Koch, 1881; *Zelotes longipes* (L. Koch, 1866). *A. psammophila* was the dominant species at one sampling site and ranked second, third, fourth, fifth or lower at other sites. The average relative frequency of *A. psammophila* was considerably higher in the Kiskunság National Park ( $0.12 \pm 0.14$  (mean  $\pm$  SD) than in the Nyírség area ( $0.04 \pm 0.05$ ), but its dominance status was very variable



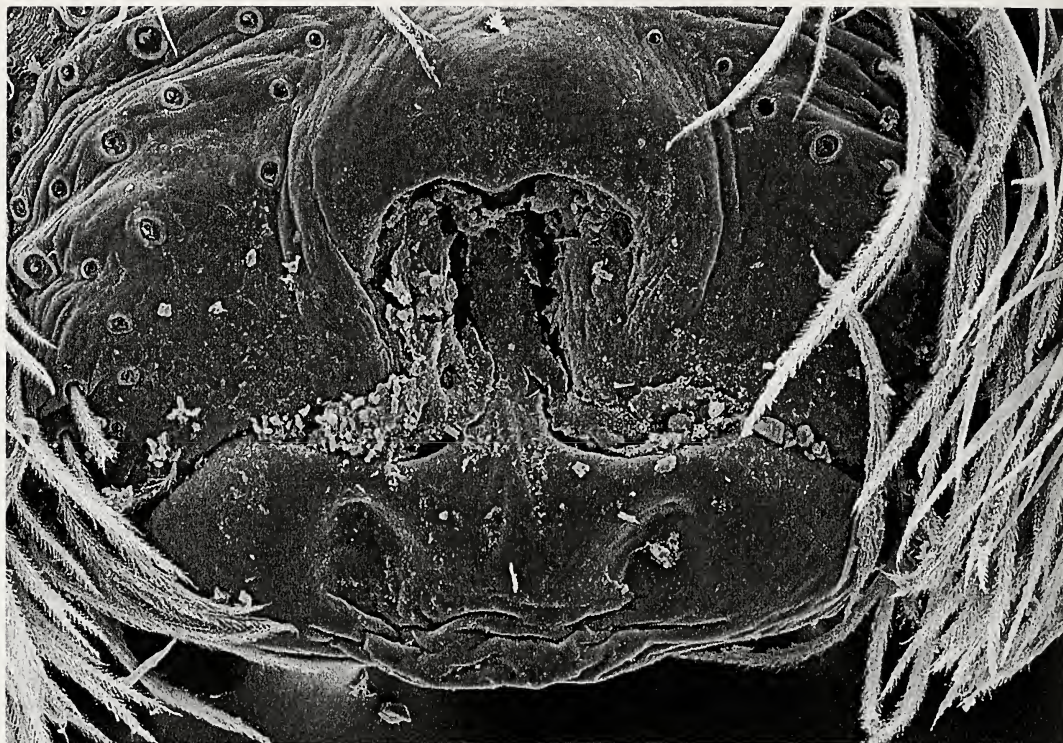


Figure 5.—Epigynum, ventral view.

even within one region. For the cohabiting species that were present at least at 50% of all the sampling sites (5 locations), we carried out an association test. The results suggest that out of the cohabiting species *A. psammophila* shows the closest relationship with *Xysticus ninnii* Thorell 1872 and *Zelotes longipes* (L. Koch 1866) as far as their environmental needs are concerned (Fig. 7).

## DISCUSSION

Morphologically, *Alopecosa psammophila* can be well distinguished from the other *Alopecosa* species in Central Europe by the highly specific three-dimensional shape of its genitalia. Phenologically, it is noted that the species shows the greatest activity in October and November. The co-occurring species of the genus (*A. cursor*, *A. cuneata* and *A. sulzeri*) have their maturity season in the summer. An exception to this is *Alopecosa accentuata* (Latreille, 1817) which similarly to *A. psammophila* overwinters as adults; thus it has adult specimens in autumn, in spring and in early summer (Nentwig et al. 2003). On the basis of the investigations carried out so far, we conclude that *A. psammophila* is a species generally and frequently occurring in the sandy grasslands of Hungarian plains in the Carpathian Basin, and that it can even be the dominant species of the ground-dwelling spider communities in these habitats. In the case of sandy grasslands in the plains we found great differences in the coverage of vegetation, coverage of lichens and mosses, cover-

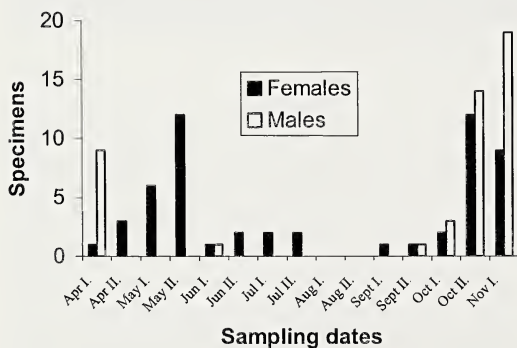


Figure 6.—Phenology of *Alopecosa psammophila* based on pitfall samples collected at Fülöpháza in 2001.



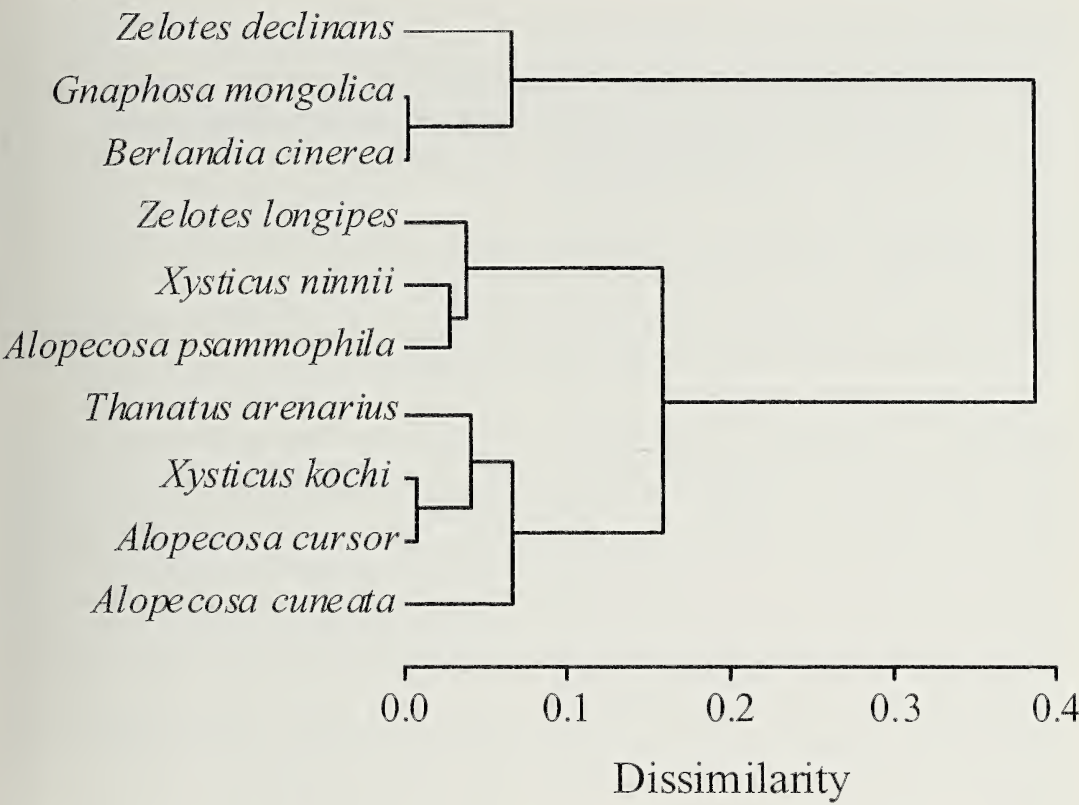


Figure 7.—The species in the closest association with *Alopecosa psammophila* in the Great Hungarian Plain (the Matusita index of similarity and the Ward-Orloci fusion method were used).

age of the sand and mosses, and in vegetation height, but these differences seemed not to affect the abundance of *A. psammophila*. We assume that the species is widespread in the dry sandy grasslands of Central Europe.

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## SIZE DEPENDENT INTRAGUILD PREDATION AND CANNIBALISM IN COEXISTING WOLF SPIDERS (ARANEAE, LYCOSIDAE)

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**ABSTRACT.** Two species of wolf spider, *Hogna helluo* (Walckenaer 1837) and *Pardosa milvina* Hentz 1844 dominate the predatory community on the soil surface of agroecosystems in eastern North America. Although as adults they are very different in size, differences in phenology ensure that they overlap in size at various times during the year. In a laboratory experiment, we explored the propensity of each species to attack and kill the other wolf spider species (intraguild predation), conspecifics (cannibalism) or crickets (ordinary predation). Both spiders attacked and killed a broader size range of crickets more quickly than they approached other spiders. We found no differences in *Hogna* foraging on conspecifics or *Pardosa*, but *Pardosa* attacked and killed *Hogna* more readily than conspecifics. Because *Hogna* was so slow in attacking other spiders, their impact as an intraguild predator may be quite small, especially if their approach to crickets is an indication of their predatory tendencies with insects. On the other hand, *Pardosa* attacked and killed small *Hogna* as readily as crickets, which suggests they may have an influence on *Hogna* populations if *Hogna* young emerge coincident with large juvenile or adult *Pardosa*.

**Keywords:** Cannibalism, intraguild predation, agrobiont spiders, predator-prey

Cannibalism and intraguild predation (IGP) are important to spider communities and have the potential to affect population sizes and/or species diversity of spiders as well as that of potential insect prey (Wagner & Wise 1996; Hodge 1999; Samu et al. 1999; Finke & Denno 2002; Matsumura et al. 2004; Denno et al. 2004). Predation is a dynamic process, the outcome of which depends on the relative sizes of the predator and prey, their physiological state, attack strategy and inherent aggressiveness (Walker et al. 1999; Persons et al. 2001; Buddle 2002; Balfour et al. 2003; Buddle et al. 2003; Mayntz et al. 2005). Many of these factors will shift over time both with age and recent experience and thus the relative importance of cannibalism and/or IGP to foraging individuals, population structure and community composition will shift as well (Wagner & Wise 1996; Balfour et al. 2003; Buddle et al. 2003). For spiders that coexist, an understanding of the situations under which cannibalism and IGP occur is critical to understanding how and when they can persist in the same habitat.

In the present study we explore the preda-

tory tendencies of two species of wolf spider (Araneae, Lycosidae) that coexist on the soil surface in agricultural fields across the eastern portion of North America. Because the species differ in size, activity, and phenology, we wanted to characterize the circumstances under which these spiders engaged in cannibalism or intraguild predation and compare those predatory interactions to attacks on insect prey. Under controlled laboratory conditions, we paired a wide size range of individuals with conspecifics, the other species of spider, or crickets and documented the outcome and timing of predation. In this way, we hoped to gain a better understanding of the specific predatory strategy of each of the spider species and the relative influence that these species have on their insect prey, which would help us to gain insight into the nature of their co-existence.

### METHODS

**Study species.**—*Hogna helluo* (Walckenaer 1837) and *Pardosa milvina* Hentz 1844 coexist on the soil surface in disturbed riparian habitats and agroecosystems throughout the



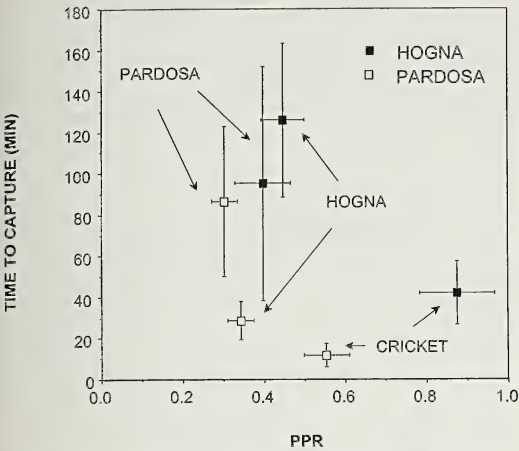


Figure 1.—Mean prey to predator mass ratio (PPR  $\pm$  S.E.) for captured prey vs. the time (min  $\pm$  S.E.) it took the prey to be captured. Trials where *Hogna* was predator are indicated by solid squares and those where *Pardosa* was predator are indicated by open squares. Specific prey types are listed with an arrow pointing to the data for that treatment.

eastern portion of North America (Dondale & Redner 1990; Marshall & Rypstra 1999; Marshall et al. 2002). *Pardosa* is small (20 mg), active, and can be found at high densities (10–15 per m<sup>2</sup>) whereas *Hogna* is large (800 mg), less active, and found at relatively low densities (1–2 per m<sup>2</sup>) in soybean fields in the midwestern section of the United States (Marshall & Rypstra 1999; Walker et al. 1999; Marshall et al. 2002). *Pardosa* is an annual species with a mid-July population peak. Except for a relatively short period during which the adults and spiderlings co-occur, the size distribution of *Pardosa* individuals active in the fields at any given time is fairly narrow (Marshall et al. 2002). On the other hand, *Hogna* seems to have a two-year life cycle with more stages occurring in the fields at the same time (Marshall et al. 2002). Although *Hogna* are usually larger than *Pardosa*, because of the variability in their life cycle, it is possible for large subadult or adult *Pardosa* to coexist with early stages of *Hogna*. Previous studies have revealed that each species readily consumes smaller individuals of the other in the laboratory (Persons et al. 2001; Balfour et al. 2003). Here we explore those predatory interactions systematically across a broad range of size ratios.

Both species of spiders were collected from corn and soybean fields at the Miami Univer-

sity Ecology Research Center (Oxford, Butler County, Ohio, USA) and held in the laboratory or reared from animals collected at that site. When not involved in experimentation, spiders were housed individually in translucent plastic cylindrical containers 8 cm in diameter with 5 cm walls with 1–2 cm of damp peat moss covering the bottom. Spiders were watered and fed once or twice weekly on a diet of crickets (*Acheta domesticus*), fruit flies (*Drosophila* spp.) and or meal worms (*Tenebrio* spp.). Containers with spiders were held in an environmental chamber between 23–25 °C on a 12:12 L:D cycle at 60–75% humidity.

**Experimental protocol.**—Spiders were randomly selected from the laboratory population and brought to standard hunger levels by feeding them *ad libitum* with *Drosophila melanogaster* for 2 days. Spiders were then held for 7 days before testing to ensure that they were similarly hungry. Spiders were randomly assigned to be paired with conspecifics (to monitor cannibalism), heterospecifics (to monitor intraguild predation) or crickets (to monitor ordinary predation). Those assigned to be paired with conspecifics were marked with a drop of acrylic paint on the abdomen or cephalothorax so that we could identify individuals. All spiders and crickets were weighed and then introduced into a testing arena simultaneously. The arenas consisted of 14 cm diameter Petri dishes with a base of dampened plaster of Paris (as in Samu et al. 1999). Animals were allowed to interact in the arena for 24 h during which time we recorded if and when predation occurred. Experiments were run in groups that included representatives of all treatments between July 1998 and July 2001.

**Statistical analysis.**—In order to determine how similar the spiders and insects used in each treatment were, we compared the mass of predators and prey across all treatments in ANOVAs. In addition, we calculated prey/predator mass ratio (PPR) by dividing the mass of the prey by the mass of the predator. In cases where there was no predation, we randomly assigned one of the spiders as prey and the other as predator using a coin toss algorithm. In order to ensure pairings were similar across treatments, PPRs were also compared in an ANOVA. The effects of predator species, prey type, and PPR on the frequency of predation were compared using a

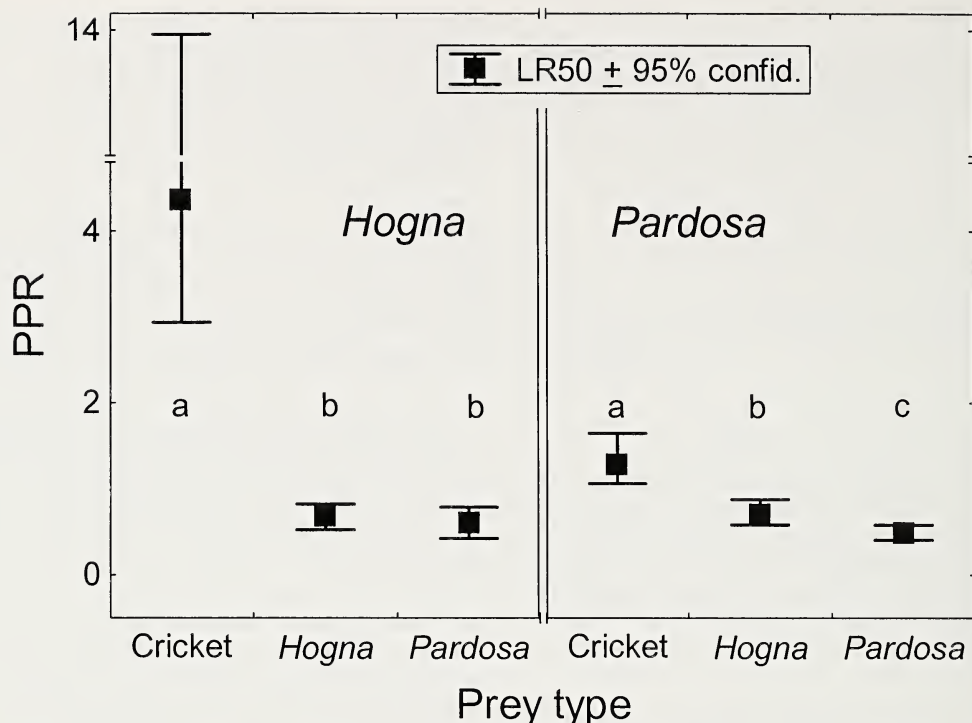


Figure 2.—Fifty percent lethal mass ratio (LR50) ( $\pm$  95% confidence interval) for *Hogna* (on the left) and *Pardosa* (on the right). Prey type is on the X-axis. Where treatments are indicated with the same small letter in the middle of each figure, the overlap of the 95% confidence ranges suggests that there was no significant difference.

logistic regression analysis. From the logistic regression, we determined the PPR at which there was a 50% likelihood of a predatory event (LR50). Differences in LR50s across treatments were evaluated by comparison of the 95% confidence intervals. The effects of the same factors (predator species, prey type, and PPR) on the time until predation were evaluated using a parametric survival analysis using the Proportional Hazards model. In this case pairwise comparisons were made using the Bonferroni test with an overall  $P$ -value of 0.05. Both the logistic regression and survival models were run initially with all interactions included. The non-significant interactions were removed after the first run and the models were run again.

We also wanted to determine if any of the observed preferences were due to size or if they had to be attributed to some other quality of the prey (e.g. nutrition, taste). We hypothesized that, if the preference was size related, then there would be a size ratio ( $PPR_{critical}$ ) below which predators would not discriminate

between prey types. We defined  $PPR_{critical}$  as the maximum PPR value where the differences between predation on two prey types were no longer significantly different ( $P = 0.05$ ). In order to find the  $PPR_{critical}$ , we started by removing the sample with the highest PPR and rerunning the statistical test, if it was still significant, we removed the sample with the next highest PPR, and ran the test again. We continued this process until the  $P$ -value associated with any difference was equal to 0.05.

## RESULTS

Overall there were no differences in the mass of the *Hogna*, *Pardosa*, or crickets used in our treatments (Predator mass  $F = 1.81$ ,  $df = 5, 401$ ,  $P = 0.11$ ; Prey mass  $F = 1.02$ ,  $df = 5, 401$ ,  $P = 0.40$ ) (Table 1). In addition, animals were paired so that the PPR values were similar across treatments ( $F = 1.71$ ,  $df = 5, 401$ ,  $P = 0.13$ ) (Table 1). Even though not significantly different, the PPR for *Hogna* on crickets was somewhat higher than the oth-



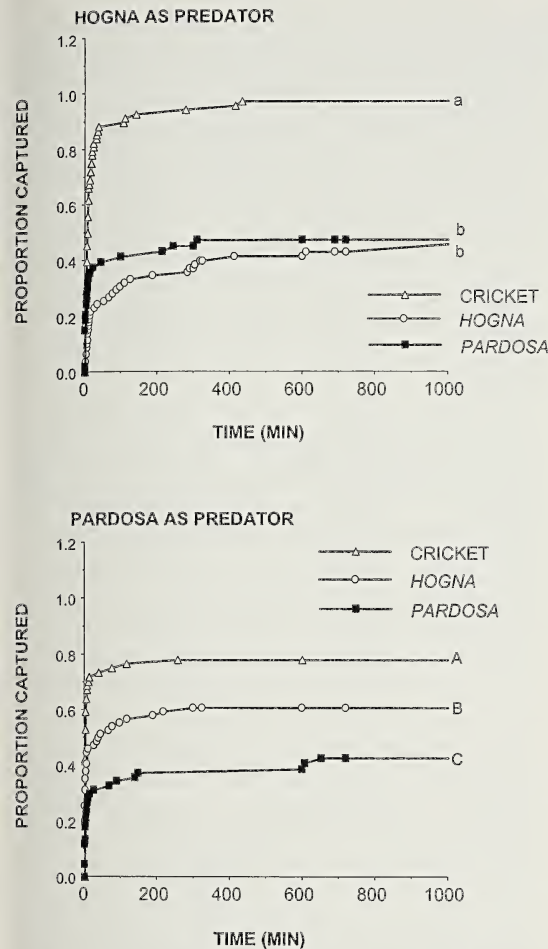


Figure 3.—Capture success over time of *Hogna* and *Pardosa* on the three different prey types. Those indicated with the same letter (at the right of the line) were not significantly different using Bonferroni comparisons with a critical value of 0.05.

ers. To some degree, this variation was intentional as we attempted to observe interactions across the complete prey size range that each spider would take. Note that even though the PPR is close to one, meaning that the prey were the same size as the predator, the capture rate is still very high (94.3%) as compared to other treatments (Table 1). Predator species, prey species and the PPR all affected the occurrence and the timing of predation in complex ways (Table 2).

**Predation on crickets vs. spider prey.**—Both *Hogna* and *Pardosa* had higher capture success on crickets than on spiders (*Pardosa*:  $\chi^2_{195} = 10.19$ ,  $P = 0.001$ ; *Hogna*:  $\chi^2_{209} = 54.54$ ,  $P < 0.0001$ ; Table 1). Both species

killed larger crickets than they killed other spiders (higher PPR) (Fig. 1). However at PPRs less than 0.54 for *Pardosa* ( $\text{PPR}_{\text{critical}}$ ,  $\chi^2_{97} = 3.82$ ,  $P = 0.05$ ) and 0.57 for *Hogna* ( $\text{PPR}_{\text{critical}}$ ,  $\chi^2_{74} = 3.46$ ,  $P = 0.05$ ) there were no differences between spider vs. cricket prey. The process by which we generated the  $\text{PPR}_{\text{critical}}$  inevitably resulted in a loss of sample size, and therefore power, however, we regard the remaining case numbers still large enough ( $N_{\text{Pardosa}} = 98$ ,  $N_{\text{Hogna}} = 75$ ) to draw valid conclusions on  $\text{PPR}_{\text{critical}}$  values. The PPR at which there was a 50% chance of a predatory event (LR50) was significantly higher for crickets than for spider prey (Fig. 2). Likewise, overall crickets were killed more quickly than other spiders (Figs. 1, 3).

**Comparing the predation strategy of *Hogna* and *Pardosa*.**—The two predators differed in their responses to the prey types tested (Table 2). *Hogna* consistently took larger prey than *Pardosa* from every prey category (Figs. 1, 2). On the other hand, *Pardosa* was consistently faster than *Hogna* in taking every prey type (Figs. 1, 3). *Pardosa* was more likely to capture *Hogna* than conspecifics ( $\chi^2_{139} = 5.53$ ,  $P = 0.018$ , Table 1) but there was no difference in the capture rate of *Hogna* on either spider species ( $\chi^2_{131} = 0.27$ , NS; Table 1). Likewise, the LR50 was larger for *Pardosa* preying on *Hogna* than it was for *Pardosa* cannibalism (Fig. 2) but there was no difference in the LR50 for *Hogna* preying on heterospecifics or conspecifics (Fig. 2). Similarly *Pardosa* captured *Hogna* more quickly than it captured other *Pardosa* but there were no differences in the *Hogna*'s predatory speed on conspecifics or heterospecific spiders (Figs. 1, 3).

## DISCUSSION

Clearly these two spider species, *Hogna helluo* and *Pardosa milvina*, differ in their foraging behavior across the various sizes of the different prey types tested here. *Hogna* is generally slower to attack and kill a potential prey but generally take prey in larger size classes than *Pardosa*. Although *Hogna* differentiated between crickets and spiders, they did not seem to differentiate between conspecifics and a common coexisting intraguild predator, *Pardosa*. On the other hand, *Pardosa* reacted differently to all three prey types; killing larger crickets faster than they killed *Hogna* and kill-

Table 1.—Summary of the sample size, capture frequency, predator mass ( $\pm$ S.E.), prey mass ( $\pm$ S.E.), and prey to predator mass ratio (PPR  $\pm$  S.E.) for each treatment.

Treatments	<i>n</i>	Number captured (%)	Predator mass (mg)	Prey mass (mg)	PPR
<i>Hogna</i> on crickets	70	66 (94.3%)	14.4 $\pm$ 1.2	14.6 $\pm$ 1.9	0.97 $\pm$ 0.11
<i>Hogna</i> on <i>Hogna</i>	78	34 (43.6%)	19.2 $\pm$ 1.2	11.7 $\pm$ 1.7	0.84 $\pm$ 0.07
<i>Hogna</i> on <i>Pardosa</i>	54	28 (48.1%)	19.5 $\pm$ 1.4	9.9 $\pm$ 2.1	0.63 $\pm$ 0.05
<i>Pardosa</i> on crickets	64	50 (78.1%)	19.6 $\pm$ 1.3	11.1 $\pm$ 1.8	0.75 $\pm$ 0.07
<i>Pardosa</i> on <i>Hogna</i>	74	44 (59.5%)	17.6 $\pm$ 1.2	9.2 $\pm$ 1.8	0.64 $\pm$ 0.06
<i>Pardosa</i> on <i>Pardosa</i>	66	38 (42.4%)	19.1 $\pm$ 1.3	12.2 $\pm$ 1.9	0.68 $\pm$ 0.06
All Groups	406	260 (64.1%)	18.4 $\pm$ 1.6	11.4 $\pm$ 2.1	0.76 $\pm$ 0.03

ing larger *Hogna* faster than they killed conspecifics.

**Predation on crickets vs. spider prey.**—

Both cannibalism and IGP have been extensively documented in wolf spiders (Wagner & Wise 1996; Samu et al. 1999; Balfour et al. 2003; Buddle et al. 2003). Because these interactions carry with them an increased risk of injury and/or reciprocal predation, we expected a different, and perhaps more cautious, predatory approach to other spiders when compared to crickets. We reasoned that the relative size of the prey to its predator (PPR) would be one measure of risk and we found that the PPR at which there was a 50% chance of a predatory event was much higher for crickets than spider prey (Fig. 2). However further exploration of the data reveals that, for both spider species, there was a PPR<sub>critical</sub> below which there were no differences in the rate of predation on spiders as compared to crickets. Thus, the significant differences in predatory strategy that we observed were due to behavioral shifts that occurred when the prey were large relative to the predator. These results confirm that relative size was more important for spider on spider contests than for attacks of crickets and suggests that both spider species were sensitive to the risk that a large predatory prey item might pose. This connection may be particularly true for *Hogna*, which easily subdued large crickets but were much slower to take smaller individuals of either spider species (Fig. 2).

Even though risk may be important to the observed differences in predation frequency, there may be other reasons for spiders to prefer insect over spider prey. It has been argued that organisms feeding on the same trophic level, and especially conspecifics, provide nu-

trients in proportions that are more closely aligned with the predator's nutritional needs (Polis 1981; Wildy et al. 1998; Fagan et al. 2002), however several studies have demonstrated that growth and survival of wolf spiders is lower when maintained on spider diets than when provided with insect prey (Toft & Wise 1999; Oelbermann & Scheu 2002; Matsumura et al. 2004). Another reason not to eat closely related species is that they may carry pathogens that can invade more easily when consumed by a conspecific or phylogenetically close host (Pfennig, et al. 1998; Pfennig 2000; MacNeil et al. 2003). Thus, selection may favor preferences for non-spider prey.

Of course wolf spiders behave differently from crickets, which may have reduced their susceptibility to capture. We attempted to control the circumstances of the interaction so that the predator had access to the same kind of sensory information in a confined space, which should minimize the small differences in capture and escape tactics. Nevertheless, it is impossible to totally uncouple the prey preferences and ease of capture from the specific signals by which the predator detects and identifies prey items (Uetz 2000; Uetz & Roberts 2002). Thus a further exploration of the role of specific sensory modalities in the predator interactions of these species is warranted.

**Comparing the predation strategy of *Hogna* and *Pardosa*.**—A variety of differences between the foraging strategies of *Pardosa* and *Hogna* have been documented (Walker et al. 1999; Walker & Rypstra 2002) and this study clarifies some additional aspects of those differences. In particular, although *Hogna* was the most effective predator on crickets, *Pardosa* distinguished between the three prey types in the proportion (Table 1), size (Figs.



Table 2.—Results of logistic regression to predict prey capture and the results of the proportional hazards survival model to predict the time it took the spiders to capture prey. Both models used predator species, prey species and prey to predator mass ratio (PPR) as predictors.

Source	df	Chi squared	P
Logistic regression model for outcome			
Whole model	7	299.782	<0.0001
Predator species	1	9.333	0.0023
Prey species	2	66.809	<0.0001
PPR	1	82.225	<0.0001
PPR * predator	1	20.895	<0.0001
PPR * prey	2	21.807	<0.0001
Survival model for time until capture			
Whole model	9	401.4444	<0.0001
Predator species	1	8.534	0.0035
Prey species	2	189.060	<0.0001
PPR	1	302.410	<0.0001
PPR * predator	1	36.730	<0.0001
PPR * prey	2	85.380	<0.0001
Predator * prey	2	14.433	0.0007

1, 2) and timing (Figs. 1, 3) of predation. *Pardosa* is a much more active species than *Hogna* (Walker et al. 1999; Walker & Rypstra 2002), which might have caused us to predict that they would be more susceptible to predation by other wolf spiders which use motion to detect prey (Persons & Uetz 1997). However, there is no evidence here to demonstrate that activity made *Pardosa* any more susceptible to the sit and wait predator, *Hogna*. In fact, it appears here that activity translated into effective search behavior that increased *Pardosa*'s ability to detect and attack more sluggish arthropod prey such as *Hogna*.

Although not significantly different, the PPRs for *Hogna* paired with crickets were somewhat higher than the other pairings because of our desire to cover the full size range of prey that each spider would attack. Thus we considered whether the longer capture times observed for *Hogna* on crickets (Fig. 1) might be due primarily to the fact that they were tested with larger prey items. However, if we compare the mean capture time for crickets larger than the *Hogna* (PPR > 1.0;  $n = 19$ ) with the capture times for those prey smaller than the *Hogna* (PPR < 1.0;  $n = 51$ ), there was no difference ( $t = 2.0$ ,  $P = 0.24$ ). This fact furthers the characterization of *Hogna* as a slow selective predator that, in the

context of the options offered here, prefers large harmless prey. On the other hand, *Pardosa* was generally faster to attack and discriminated more finely between the three prey options we included in this study.

**Implications for species co-existence in the field.**—These results may be especially important for agrobiont spiders, such as *Hogna* and *Pardosa*, as they may be important agents of biological control. The fact that crickets were more susceptible to predation across a much larger size range than spider prey suggests that the influence that two wolf spider species have on one another may not be exceedingly strong when alternative insect prey are abundant. To fully assess the field importance of these interactions, our findings need to be interpreted in the context of the life history of natural populations. Unfortunately, in spite of existing field surveys (Marshall & Rypstra 1999; Marshall et al. 2002), the life histories of the two species seem to be highly variable and, as a result, are not well enough understood to be predictable. Nevertheless, the available data suggest that *Hogna* typically has a two or three-year life cycle with several juvenile stages coexisting and *Pardosa* is an annual species with a narrower size distribution at any given time in the season. Thus, all life stages of *Pardosa* have the potential of coexisting with larger *Hogna* whereas only when *Hogna* spiderlings emerge at times of the year when large juveniles and adult *Pardosa* are around, do *Hogna* face predation risk from *Pardosa*. Although the trials suggest that *Hogna* exert modest predatory pressure on both conspecifics and *Pardosa*, their attacks were very slow (Figs. 1, 3). As a consequence, *Hogna* may not exert much predation pressure on a quick wolf spider like *Pardosa* that in an open field situation could run away. On the other hand, *Pardosa* appear to prey on small *Hogna* as quickly as on crickets, so *Hogna* that emerge and attempt to go through the first few instars during the early summer, when *Pardosa* are adults, maybe severely impacted by *Pardosa* predation. Clearly further explorations of the interactions between these two species in more natural situations are required to fully quantify their influence on one another, the nature of their coexistence and their potential role in the ecosystem.

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## REVIEW OF THE ORIENTAL WOLF SPIDER GENUS *PASSIENA* (LYCOSIDAE, PARDOSINAE)

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**ABSTRACT.** The pardosine genus *Passiena* Thorell 1890 is redefined and relimited. *Passiena* has excellent diagnostic characters, in particular the male pedipalp that carries a unique group of soft spicules on the distal part of the palea. The female of the type species, *Passiena spinicrus* Thorell 1890 from Malaysia, is illustrated for the first time. A new species, *P. torbjoerni*, is described from Thailand. All specimens of *Passiena* were collected from the ground layer of or nearby dense jungle or bush, an exceptional habitat for Oriental Pardosinae. Males of *P. torbjoerni* carry modified setae on the ventral side of the abdomen, similar to *Hygrolycosa rubrofasciata* (Ohlert 1865) and *Pardosa sphagnicola* (Dahl 1908), where they play an important role in the courtship behavior of males. Five African species currently listed in *Passiena* do not conform to the generic diagnosis as provided here. Three of these show clear affinities with *Pardosa* C.L. Koch 1847 and are consequently transferred from *Passiena*: *Pardosa praepes* (Simon 1885); *Pardosa elegantula* (Roewer 1959) new combination; and *Pardosa upembensis* (Roewer 1959) new combination. *Passiena auberti* (Simon 1898) and *Passiena albipalpis* Roewer 1959 are considered *incertae sedis* pending a generic revision of African Lycosidae as they cannot be placed with certainty into any other lycosid genus.

**Keywords:** Taxonomy, systematics, Pardosinae, ventral abdominal setae, acoustic communication

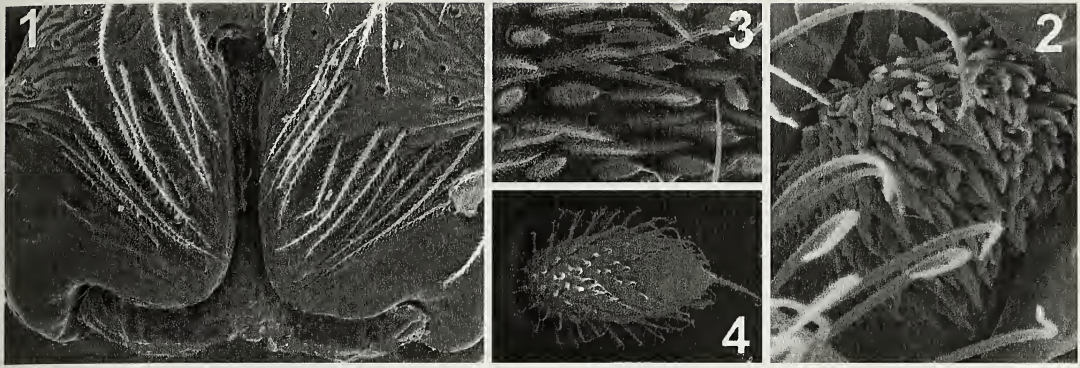
Since its original description, the systematic position of the wolf spider genus *Passiena* Thorell 1890 has remained problematic. The knowledge of characters of the male pedipalp is crucial for an interpretation of lycosid relationships (e.g. Dondale 1986; Zyuzin 1993) but only the female of the type species was known. In his revisionary work on worldwide lycosids, Roewer (1955, 1959, 1960) neglected the importance of characters of the copulatory organs at generic level, and a strong emphasis on minor details in variable somatic characters (especially eye pattern, cheliceral dentition and spination of legs) led to numerous, ill-founded taxonomic changes to the lycosid classification. For example, purely the presence of more than three pairs of ventral spines on the tibiae led him to the suggestion that *Passiena* from Oriental region should be synonymized with the subarctic-alpine Palearctic genus *Acantholycosa* Dahl 1908 (Roewer 1959).

Simon (1898) listed *Passiena* as synonym of *Pardosa* C.L. Koch 1847, noting the similarity of the type species, *P. spinicrus* Thorell 1890, with *Pardosa bifasciata* (C.L. Koch 1834) and *Pardosa auberti* Simon 1898. Subsequently, Roewer (1955) wrongly attributed

to Simon (1898) the inclusion of the latter two species in *Passiena* (see also Tongiorgi 1966) and added *Pardosa schenkeli* Lessert 1904, a close relative of *P. bifasciata*, to *Passiena*. Bonnet (1958) synonymized *Passiena* with *Pardosa*, probably without personal study of the type species. Roewer (1959) did not accept this synonymy, listed *P. auberti* and *Pardosa praepes* Simon 1885 in *Passiena* and described three new species from Africa, *P. albipalpis* Roewer 1959, *P. elegantula* Roewer 1959 and *P. upembensis* Roewer 1959. Tongiorgi (1966) was the first to note that the genital organs of the group around *P. bifasciata* were different from the African species of *Passiena sensu* Roewer (1959) when he included *P. bifasciata* and *P. schenkeli* in his revision of Italian *Pardosa*. Tanaka (1993) listed *Passiena* as a junior synonym of *Pardosa* without justification. This was not accepted by Platnick (2005) who, prior to this study, included six species in *Passiena*: *P. spinicrus*, *P. auberti*, *P. praepes* and the three species described by Roewer (1959).

The aim of this study is to provide a modern diagnosis for *Passiena* based on genital and somatic characters of the Oriental type species of which SEM photographs of diag-





Figures 1–4.—Diagnostic features of *Passiena*, SEM photographs. 1–4. *Passiena torbjoerni* paratypes, Nam Nao National Park, Phetchabun Province, Thailand: 1. Epigynum, female; 2. Tip of male palea with soft pointed spicules; 3–4. Modified setae on venter of male (cf. *Hygrolycosa rubrofasciata* in Kronstedt 1996: figs. 17, 18).

nostic characters are presented. Three of the African species incorrectly placed in *Passiena* are transferred to *Pardosa*, whereas the remaining two are considered *incertae sedis* pending revisional studies of the main African groups of the Pardosinae.

#### METHODS

All specimens of *Passiena* were examined with an OLYMPUS SZH stereomicroscope. Scanning Electron Micrographs photographs of male and female genitalia and the specialized ventral abdominal setae of the male of *P. torbjoerni* were taken with a JEOL JSM-5200 and digitized using the software package SemAfore (JEOL Ltd., Tokyo). The digital photographs were taken with an Olympus digital camera and enhanced using the “Helicon Focus” software. A critical evaluation of the African species *Passiena praepes* (Simon 1885) and *P. upembensis* Roewer 1959 was possible by comparing the descriptions with material of related African species of Pardosinae and Wadicosinae available for comparison.

Paratypes will be deposited in Stockholm (NHRS), Washington (NMNH) and Paris (MNHN).

**Terminology.**—The terminology of the structures of the copulatory organs is problematic in spiders as presumed homology and similar function and topography of structures have led to deviating nomenclatures. Zyuzin (1993) used functional (embolus, conductor) but also topographical terms (terminal apophysis, tegular apophysis) for the male pedipalp structures. Vogel’s (2004) terminology was

based on previous concepts of Dondale & Redner (1990) and seemed to be a mixture of topography, function and homology, with the exception of embolus, palea and median apophysis, all of which are strictly based on homology. Their median apophysis should not be confused with various similarly named pedipalp structures in other families of different main lineages of spiders. To avoid any confusion, the term tegular apophysis is used here instead of median apophysis. The term terminal apophysis is here used for all separate sclerites, which topographically correspond to the terminal apophysis of the Pardosinae *sensu* Dondale & Redner (1990). Additional sclerites between the tegulum and palea are not named here, as Zyuzin’s (1993) term synembolus and several “lamellae” were especially created for Lycosinae, and their application to Pardosinae might be misleading.

**Abbreviations.**—*Collections*: MZT, Zoological Museum, University of Turku, Turku, Finland; NHRS, Naturhistoriska Riksmuseet, Stockholm, Sweden; PTL, personal collection of the author. *Morphology*: AME, ALE, anterior median and lateral eyes; PME, PLE, posterior median and lateral eyes.

#### SYSTEMATICS

##### Subfamily Pardosinae Simon 1898

##### *Passiena* Thorell 1890

*Passiena* Thorell 1890: 140. Thorell 1892: 186; Simon 1898: 355; Roewer 1955: 198; Roewer 1959: 182; Bonnet 1958: 3439 (as synonym of *Pardosa*). *Pardosa* C.L. Koch 1847. Bonnet 1958: 3423; Tanaka 1993: 262.



**Types species.**—*Passiena spinicrus* Thorell 1890 by original designation and monotypy.

**Diagnosis.**—*Passiena* is mainly characterized by a combination of genitalic and somatic characters of males. It can be distinguished from all other lycosid genera by the presence of a group of soft spicules on the distal part of the palea of the male pedipalp (Figs. 2, 18). The ventral side of the abdomen in males (Figs. 3, 4) carries unique modified setae that differ considerably from similar structures in *Pardosa sphagnicola* (Dahl 1908) and *Hygrolycosa rubrofasciata* (Ohlert 1865), although their function could be similar. The base of female epigynum has variable sclerotizations of the lateral plates, although the basic pattern is typically that of Pardosinae.

**Description.**—Small to medium spiders. Color pattern of both carapace and abdomen with a wide, light longitudinal median band (Figs. 5, 7, 11, 13); fovea on carapace very distinct and dark in color. Anterior eye row slightly procurved, AME and ALE subequal in size (Figs. 9, 14); PME row narrower than that of PLE (as in most Pardosinae) (Figs. 5, 13). Femora with oblique or irregular annulations in females (Figs. 6, 8, 15), males with different color pattern on femora I (Fig. 12), distal segments of legs uniform in color, sometimes a marmorous pattern on tibiae I. Tibiae of leg I and II with 4–6 pairs of ventral spines, and metatarsi of legs I–II with usually 4 exceptionally long pairs of ventral spines. Dorsal and lateral spines conspicuous in all legs, relatively shorter in males than females. Abdomen of males ventrally with short modified setae which carry secondary hair-like structures (Figs. 3, 4). Leg spination of male weaker than that in female. Subtegulum small, distally and laterally surrounded by tegular base (Fig. 17); tegular apophysis very short and distinctly separated from tegulum by a deep furrow on all sides; terminal apophysis bipartite, embolus distally curved and partly flattened.

**Ecology.**—The habitat for all samples of *Passiena* spp. collected by myself is very dark jungle, representing a very unusual habitat for tropical Pardosinae and even for most Lycosidae except Venoniinae (pers. obs.).

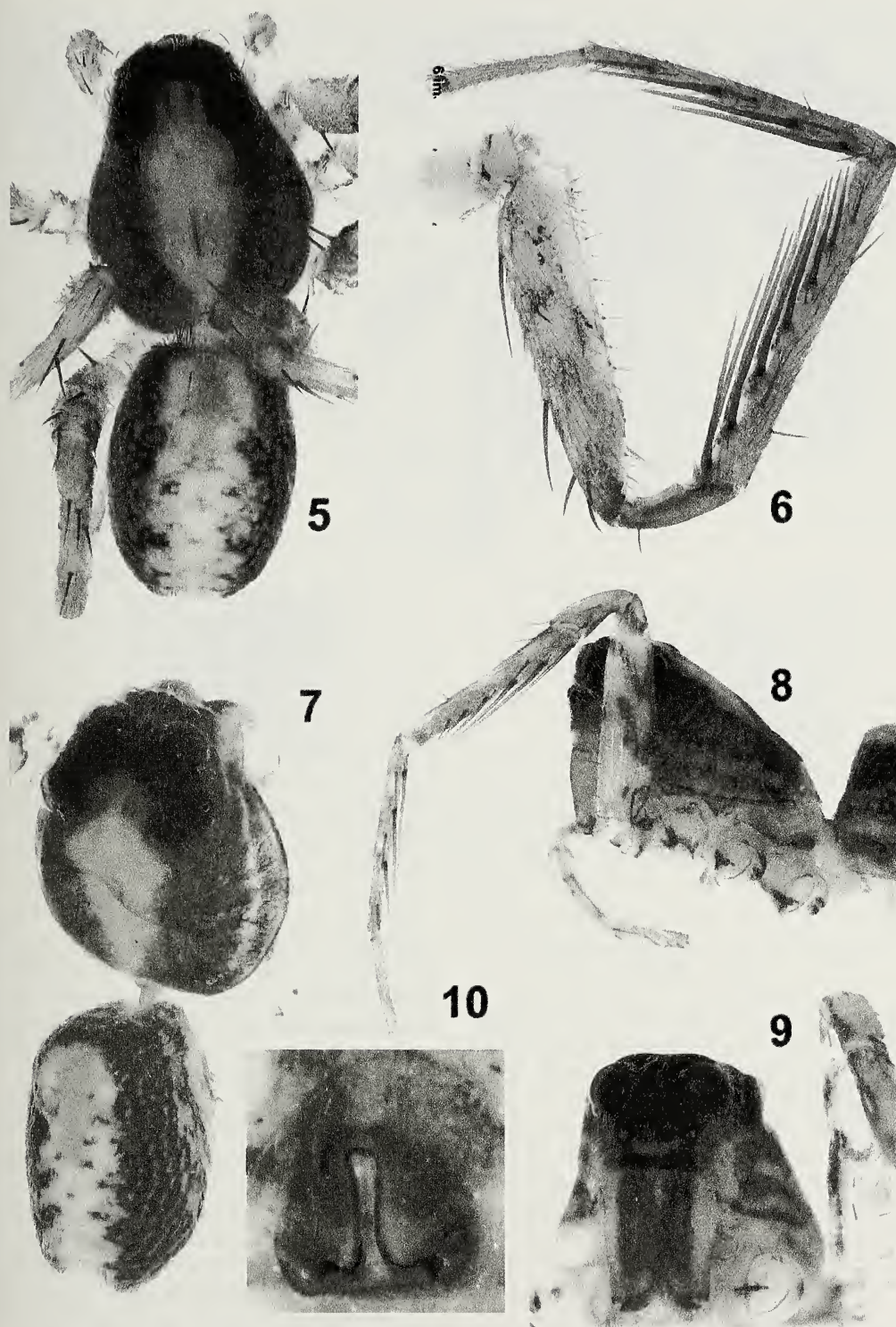
**Remarks.**—*Passiena* is retained in the Pardosinae because the male pedipalp morphology agrees at least partly with the synapo-

morphies listed by Dondale (1986) ('conductor shaftlike, lying transversely along the basal margin of the palea').

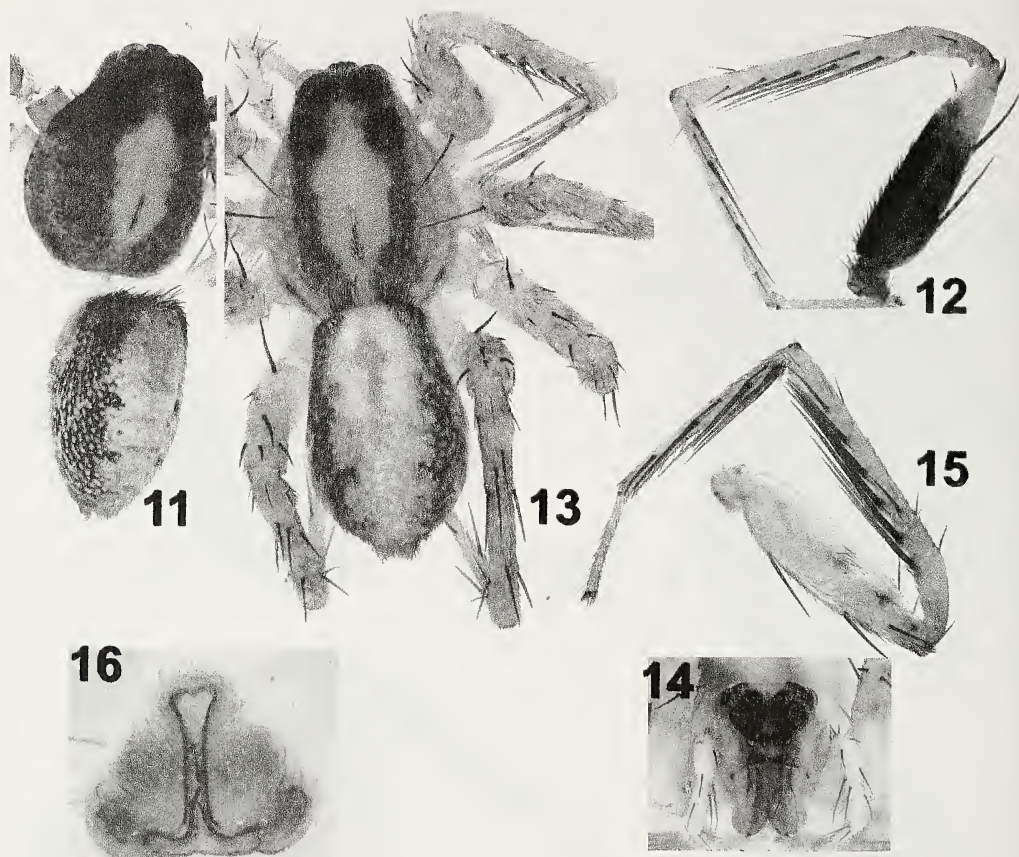
Two other wolf spider species have modified setae on the ventral side of the male abdomen, *H. rubrofasciata* and *P. sphagnicola*. In *H. rubrofasciata*, these setae play an important role during the courtship of males, which is characterized by continuously drumming the abdomen on the ground (e.g. Kronstedt 1984, 1996; Kotiaho et al. 1996; Kotiaho 1997). Similar drumming behavior has been reported in *P. sphagnicola* (Kronstedt 1996), but not studied in as much detail. Acoustic communication with other abdominal structures and legs plays an important role in the reproductive biology of spiders (Uetz & Stratton 1982). Unfortunately, no observations on the courtship behavior are available for *Passiena* spp. Although the function of the modified ventral setae appears to be similar for all above species, the ultrastructure of these modified setae is very different (for *H. rubrofasciata* see Kronstedt 1996: figs 14–18).

The possibility of synapomorphy is excluded for the ventrally spiny male abdomen, and the ultrastructure of these modified setae among normal setae is not even similar (cf. Figs. 3, 4 with Kronstedt 1996: figs 14–18). *Passiena torbjoerni* and *Pardosa sphagnicola* both belong to Pardosinae, but the males of the closest relatives of the latter (*P. pullata* group) have fewer significant modifications in their ventral setae, consisting of uneven length, insignificant thickening and differences in coloration (Holm & Kronstedt 1970; pers. obs.). *Hygrolycosa rubrofasciata* is not regarded as a member of Pardosinae (Dondale 1986; Zyuzin 1993), although the phylogenetic relationships of this genus have not been clarified. The corresponding structures and behavior of the East Asian *Hygrolycosa umidicola* Tanaka 1978 are not known to me while all other species now assigned to *Hygrolycosa* are known either as female or juveniles only and their generic placement is dubious (cf. Kronstedt 1996). The ultrastructural modification of the dorsal abdominal setae of female lycosids for attachment of the newly hatched spiderlings was documented by Rovner et al. (1973: figs. 3 a–c). All these results seem to prove that the abdominal setae of Lycosidae are easily modified for variable adaptations.





Figures 5–10.—Digital photographs of female *Passiena spinicrus* from Malaysia, Pinang; 5. dorsal view of carapace and abdomen; 6. Leg I; 6–10. Female of *P. sp.* from Sabah, Tawau; 6. Dorsal view of carapace and abdomen; 7. Dorso-lateral view of carapace and abdomen; 8. Lateral view of carapace and leg I; 9. Frontal view of carapace and chelicerae; 10. epigynum, ventral view.



Figures 11–16.—*Passiena torbjoerni* new species from Nam Nao National Park., Thailand, digital photographs; 11. male dorsally; 12. leg I of male; 13. female dorsally; 14. frontal view and chelicerae of female; 15. leg I of female; 16. epigynum.

*Passiena spinicrus* Thorell 1890

Figs. 5–10

*Passiena spinicrus* Thorell 1890: 140. Thorell 1892: 186; Simon 1898: 355; Roewer 1955: 199; Roewer 1959: 162.

*Pardosa spinicrus* (Thorell). Bonnet 1958: 3423, 3439; Tanaka 1993: 262.

**Type material examined.**—Holotype female from Pulau Pinang, Malaysia [5°25'N, 100°20'E], O. Beccari and E. D'Albertis (NHRS) [erroneously reported lost by Roewer (1959)].

**Other material examined.**—MALAYSIA: 1 ♀ with cocoon, 1 juvenile, Pulau Pinang, Batu Ferringgi, 5°28'N, 100°15'E, 29 November 1976, P.T. Lehtinen, fern thicket (MZT). A female specimen from Malaysia, Sabah, Tawau district, Bal Estate, 3°46'N, 100°59'E, 3 November 1979, rubber plantation, P.T. Leh-

tinen (MZT AA7373) with an exactly similar color pattern of the carapace, but slightly deviating spination of legs may belong to this species, although the large, well-collected gap between these localities may suggest a new taxon for the specimen from Sabah.

**Diagnosis.**—It is not possible to diagnose males of the two *Passiena* species as males of *P. spinicrus* are not known. Female *Passiena spinicrus* are distinctly smaller than *P. torbjoerni* and the central epigynal septum is more distinct in its posterior part, while the basal integument under the lateral epigynal plates is partly sclerotized, contrasting to the completely soft integument in *P. torbjoerni*.

**Description.**—Female (Pulau Pinang, Malaysia): Medium to small-sized pardosine species. Color pattern of both carapace and abdomen with wide light longitudinal band (Fig. 5) and narrow light submarginal bands,



fovea on carapace very distinct and also recognizable for its dark color; a pair of dark elongate spots within the narrower anterior part of the central band similar to the color pattern of this area in the specimen from Tawau (Figs. 5, 7); leg femora with irregular annulations (Fig. 6), the corresponding annuli in the Tawau specimen very distinct (Fig. 8); all more distal segments of legs of uniform color or sometimes with an obscure marmorous pattern of the front tibiae. Anterior eye row weakly procurved, AME and ALE subequal in size. Posterior eye row an anteriorly strongly narrowed trapezium (as in most *Pardosiinae*). Front tibiae (I–II) with 6, metatarsi I–II with 4 exceptionally long pairs of ventral spines. Dorsal and lateral spines conspicuous in all legs.

Female (Tawau, Sabah): Body total length 3.4 mm. Carapace 1.9 mm long, 1.0 mm wide. Leg I: femur 1.4, patella 0.60; tibia 1.25; metatarsus 1.25; tarsus 0.7 mm. Anterior eye row distinctly procurved, AME larger than ALE. Posterior eyes form an anteriorly strongly narrowed trapezium; PLE larger than PME. Labium much wider than long. Carapace brown, long median light stripe with a short triangle extending between the posterior eyes and a long light, gradually tapering triangle extending close to the posterior margin. Narrow light submarginal stripes are present. Chelicerae mesally brown, laterally light, sternum and coxae dirty white, gnathocoxae and labium uniform light brown. Remaining femora (I and IV) with three dark very oblique U-shaped annulations, patellae and tibiae brown with lighter marmorous pattern, metatarsi and tarsi (I and IV) uniformly pale yellowish brown.

Lateral faces of abdomen rather dark brown with regularly placed minute pale spots, central light stripe wide with dark segmentally arranged lateral dentations, the anterior folium yellowish brown, slightly sclerotized. Ventral face of abdomen with wide central light band, its margins with numerous dark dentations. Two pairs of very distinct circular muscular apodemes behind the epigastric fold. Epigynal area distinctly darker than its surroundings.

Spination of leg I: 5 ventral pairs of very long spines on tibia and 3 ventral pairs of very long spines on metatarsi, (both legs II and III missing) 2 shorter retrolateral spines are present both on tibiae and on metatarsi I. Nu-

merous short erect setae on ventral side of femur I among 4 stronger and longer setae.

Epigynum: shape of epigynal plates as in Fig. 10 (Tawau specimen: the epigynal mount of the MZT specimen from Pinang, compared with the topotypical holotype has not been found during this study). Epigynal septum anteriorly rounded in ventral view, weakly sclerotized pair of inner arches (corresponding to margins of anterior pockets of most lycosid species). Vulva with two pairs of rounded receptacula, connected to each other with a short constriction only. Epigynal median furrow anteriorly rounded and slightly widened; posterior transverse bar well developed. Lateral epigynal plates with a distinct notch bordering the posterior bar.

Male: unknown.

Egg-cocoon (Pulau Pinang, Malaysia): light brown and with a distinct surface fold or seam as in all *Pardosa* s. lat.

**Distribution.**—*Passiena spinicrus* is found on Pinang Island, Malaysia, and possibly in northeastern Borneo. The present study confirms the presence of a population at the type locality Pulau Pinang still in 1976. I have also seen juvenile specimens from the Malayan Peninsula that may be referable to this species. The identification of juvenile specimens of *Passiena* at the generic level is possible in the field due to the unusual color pattern and leg spination, and the unusual habitat preference. In contrast to most other tropical wolf spider species, *P. spinicrus* occurs in exceptionally dark habitats, in the ground layer of dense jungle or bush.

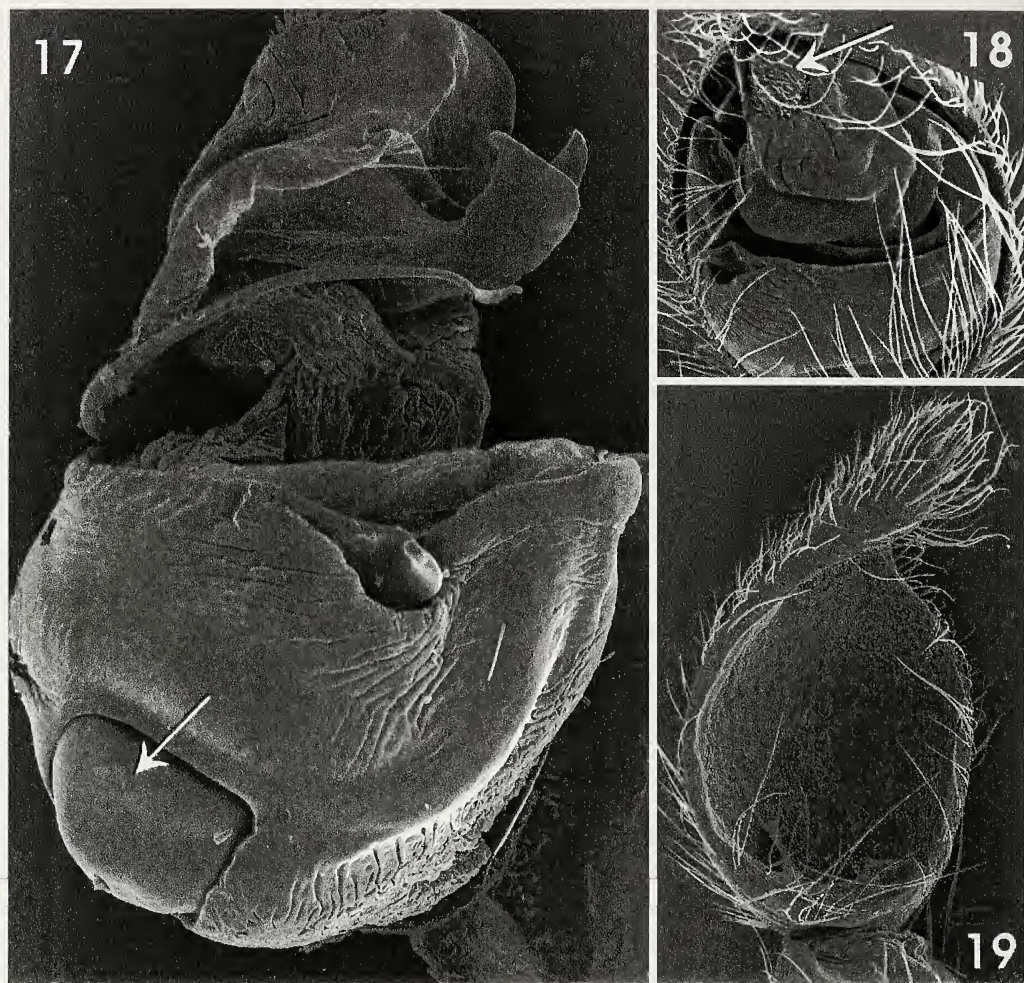
Roewer (1955) and subsequently Platnick (2005) listed a much wider range ('India to Hong Kong, Sumatra, Sulawesi') which seems to be erroneous since the original description of the holotype female from Malaysia, Pulau Pinang, appears to be the only previous published record. In addition, I have not found *P. spinicrus* during extensive fieldwork in Sumatra, India and neighboring countries, or in Sulawesi and Hong Kong, although I have specifically searched for rainforest dwelling pardosines for many years.

*Passiena torbjoerni* new species

Figs. 1–4, 11–19

**Material examined.**—Holotype male, Nam Nao National Park, Phetchabun Province, Thailand, 16°43'N, 101°33'E, 19 November





Figures 17–19.—*Passiena torbjoerni* new species from Nam Nao National Park, Thailand, SEM-micrographs of male palp: 17. bulb ventrally, arrow = subtegulum; 18 distal view of palp, arrow = spicules on palea; 19. cymbium, bulb removed, ventral view.

1976, P.T. Lehtinen, ground layer of savanna (NHRS). Paratypes: THAILAND: 1 ♂, collected with holotype (NHRS); 3 ♂, 4 ♀, 2 juveniles, Nam Nao National Park, Phetchabun Province, 16°43'N, 101°33'E, 19 November 1976, P.T. Lehtinen, bamboo thicket (1 ♂, 1 ♀ PTL; remainder in NHRS); 1 ♂, 1 juvenile, same locality, 29 October–19 November 1976, pitfall trap, J. Ruohomäki, E. Huitula, P.T. Lehtinen, grassy margin of bamboo forest (NHRS); 1 subadult ♂, same locality, 29 October–19 November 1976, pitfall trap, J. Ruohomäki, E. Huitula, P.T. Lehtinen, grassy forest (PTL); 1 juvenile, Doi Suthep, Kontathon waterfall, Chiangmai Province, 18°49'N, 98°54'E, 14 November 1976, P.T. Lehtinen, in jungle (PTL).

**Etymology.**—This species is dedicated to the Swedish lycosid specialist and my good friend Dr. Torbjörn Kronestedt, one of the few specialists who has seen a real *Passiena*.

**Diagnosis.**—It is not possible to diagnose males of the two *Passiena* species as males of *P. spinicrus* are not known. Females of *Passiena torbjoerni* are distinctly larger than those of *P. spinicrus* and the central epigynal septum is less distinct posteriorly, while the basal integument under the lateral epigynal plates is desclerotized, contrasting to partly sclerotized integument in *P. spinicrus*.

**Description.**—Male (from Nam Nao National Park, Thailand): Total body length 4.2 mm (including lengthened/outdrawn petiolar tube). Carapace 1.65 mm long, 1.58 mm wide.



Abdomen 2.1 mm long. Leg I: femur 1.96; patella 0.56; tibia 1.47; metatarsus 1.61; tarsus 0.81 mm. Carapace with laterally steep cephalic region (Fig. 14); clypeus ca. three times the diameter of AME; dorsally with a centrally widened, very pale-brownish longitudinal median band, while the lateral parts are dark brown without further signs of pattern (Fig. 11) with a wide pale longitudinal band; median band continuing into the cephalic area after a dark constriction caused by the very dark brown surroundings of the posterior eyes, lateral parts uniform dark brown. Some specimens have faint narrow submarginal lighter stripes; posterior eyes on blackish wide tubercles; sternum, labium and gnathocoxae uniform light brown. Fovea conspicuous, dark. Chelicerae with longitudinal dark stripes as in *P. spinicrus*.

Abdomen (Fig. 11) with a reddish brown central longitudinal band, its margins unevenly serrate. Lateral parts brown, throughout with minute lighter spots. Ventral face of abdomen pale brown, its central area throughout covered with short spines (Figs. 3, 4).

Femora and tibiae of all legs with numerous dorsal and lateral spines, some dorsal spines on femora exceptionally long. Tibiae and metatarsi I–II with 3–4 pairs of ventral spines (Fig. 12), but these spines are much shorter than the corresponding spines on females of both known species of *Passiena*. Basal two thirds of femora I dark brown in dark specimens (Fig. 12), with oblique dark stripes on lighter specimens, other segments uniform pale brown.

Male pedipalp (Figs. 17–19) dark brown, with conspicuous field of soft spicules in the distal part of palea (Figs. 2, 18). Cymbium distally screwed (Fig. 19); tegular apophysis short, terminal apophysis bilobate, embolus distally curved and flattened. The group of spiculae in the distal part of palea deviates from all modifications of palea in other Pardosine groups, where all paleal modifications are well sclerotized.

Female (paratypes from Nam Nao National Park): Total length 4.2 mm. Carapace 2.21 mm long, 1.65 mm wide. Abdomen 2.2 mm long. Leg I: femur 1.75; patella 0.56; tibia 1.82; metatarsus 1.65; tarsus 0.74 mm. Carapace dorsally with a centrally widened, pale-brownish longitudinal median band bordered by a pair of dark brown longitudinal bands.

The lateral parts have regularly additional pale submarginal bands as pale-colored males (Fig. 13); of PME and PLE; chelicerae pale with very distinct dark central stripes on the anterior face as in *P. spinicrus*. Row of anterior eyes slightly procurved, AME larger than ALE (Fig. 9). Abdomen dorsally with a very wide pale-brown central field, laterally with narrow stripes forming a dark brown reticulation; anterior margin encircled by a row of dark setae; venter and sternum uniform pale brown. Basal half of femora I dark brown; all other femora may have an indistinct dark marmorous pattern; all other leg segments more or less uniform pale brown. Spination of legs: All femora with two strong dorsal spines and 2–3 short lateral spines on both sides; tibiae I–II with six long, strong pairs of ventral spines, one long retrolateral spine, and one subdistal dorsal spine; metatarsi I–II with 3 pairs of very long ventral spines in the basal half and few shorter ventral and lateral spines; patellae, tibiae and metatarsi III–IV irregularly covered with comparatively weak and short spines, very different from the very long and strong ventral spines of legs I–II.

Epigynum: narrow, soft median septum between lateral plates continued as a soft basal transverse bar; median septum inverted-T shaped; posterior basal transverse bar with slightly curved lateral arms.

**Remarks.**—*Passiena torbjoerni* is found in Phetchabun and Chiangmai Provinces of Thailand, where it inhabits the floor of rainforests.

## DISCUSSION

**The African *Passiena*.**—All current African representatives of *Passiena* except *P. auberti* have a dorsal abdominal pattern with an anterior folium, followed by an unpaired dark central area. In addition, their genitalia do not resemble in any way *P. spinicrus* or *P. torbjoerni* suggesting that they are misplaced in *Passiena*. Critical evaluation of the genital and somatic characters of three of these species allowed a tentative placement in other lycosid genera pending a generic revision of African Lycosidae.

***Passiena praepes* (Simon 1885).**—This species is only known from the female type specimen collected in Senegal (Simon 1885) and was originally described in the genus *Pardosa*. Its transfer to *Passiena* by Roewer (1959) was primarily supported by the pres-

ence of four pairs of ventral spines on tibia I. The drawing of the epigynum (Roewer 1959: 170, fig. 86a) strongly resembles that of *P. micheli* Simon 1901 (Roewer 1959:67, fig. 23a) and *P. potteri* Simon 1901 (Roewer 1959:70, fig. 27a) both of which are regarded as junior synonyms of *P. naevia* (C.L. Koch 1875), a typical representative of the *Pardosa nebulosa*-group (Alderweireldt & Jocqué 1992). The abdominal pattern of *P. praepes* as illustrated by Roewer (1959) confirms its affinities with the *P. nebulosa* group. Therefore, *P. praepes* is here regarded as a representative of the *Pardosa nebulosa* group, and consequently returned to the genus *Pardosa*.

***Passiena auberti* (Simon 1898).**—This species from South Africa was originally described in *Pardosa* (Simon 1898). Due to a distinct and wide longitudinal pale band both on carapace and abdomen, combined with a strongly procurved anterior eye row it does not fit into any currently described group (genus or species group) of the Pardosinae. Pending a generic revision of African Lycosidae, I regard *P. auberti* as *incerta sedis*.

***Passiena albipalpis* Roewer 1959.**—This species from Cameroon has six pairs of ventral spines on tibiae I and II, an unusual type of tegular apophysis and a strongly sclerotized and widely arched palea on the male pedipalp. I am unable to place this species into any known genus within the Pardosinae. However, the somatic characters and male and female genitalia are very different to the two known species of *Passiena*, and therefore I regard this West-African species as *incerta sedis*.

***Passiena elegantula* Roewer 1959.**—This species from the Democratic Republic of Congo is known from both sexes and Roewer's (1959:236, fig. 118) illustrations including the male pedipalp with its enlarged palea region suggest a placement in *Pardosa*. In addition, it does not display the typical carapace and abdomen coloration of *Passiena* with the typical wide light bands. Consequently, *P. elegantula* is here transferred to *Pardosa*: *P. elegantula* (Roewer 1959) NEW COMBINATION.

***Passiena upembensis* Roewer 1959.**—This species is known from a female collected in the Democratic Republic of Congo. It is certainly related to *Pardosa oncka* Lawrence 1927 and *Pardosa crassipalpis* Purcell 1903 and may be a junior synonym of the latter. Similarly, Kronestedt's (1987) revision

showed that the widespread *P. oncka* was illustrated under six differently named species by Roewer (1959). However, I have not compared the type of *P. upembensis* with material of *P. crassipalpis* from Botswana available to me. Kronestedt (1987) suggested a potential placement of *P. oncka* in *Wadicosa* Zyuzin 1985. Here, I transfer *P. upembensis* to *Pardosa*, *P. upembensis* (Roewer 1959) NEW COMBINATION, based on its similarity with *P. oncka* and *P. crassipalpis* pending a revision of the African Pardosinae and Wadicosinae.

#### ACKNOWLEDGMENTS

Dr. Torbjörn Kronestedt (NHRS) provided the opportunity to study the type material of *P. spinicrus* during my visits to Stockholm, and supplied loans of other Oriental pardosine species. Reijo Hakanen and Eirik Granqvist, both at the time at the University of Helsinki, put in substantial efforts to collect spiders in Botswana in 1973, resulting in rich material of African Pardosinae for comparative studies at our museum. Dr. Yuri Marusik (Magadan, Russia) assisted in the digital photography and numerous computer problems. Mr. Veikko Rinne (University of Turku) also assisted with computing issues. Dr. Volker Framenau (Western Australian Museum, Perth) succeeded to direct my arachnological activities again to Lycosidae and he and an unnamed referee also gave valuable suggestions and editorial advice on the manuscript. This article is a product of his invitation to the Lycosidae Symposium held during the International Congress in Gent in 2004.

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## THE FUNCTION OF LONG COPULATION IN THE WOLF SPIDER *PARDOSA AGRESTIS* (ARANEAE, LYCOSIDAE) INVESTIGATED IN A CONTROLLED COPULATION DURATION EXPERIMENT

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**ABSTRACT.** Copulation duration varies greatly in wolf spider species, ranging from a few seconds to several hours. In *Pardosa agrestis* (Araneae, Lycosidae), the most common ground dwelling spider in Central European fields, copulation typically takes more than two hours. Since long copulation is likely to entail certain costs, we address the question, “what is the function of long copulations?” We investigated the consequences of lengthy copulation in an experimental situation, where copulations either ended spontaneously, or were interrupted after 10 min, 40 min or 90 min. There was no difference in the number of offspring per female when treatments were compared and we conclude that ten minutes of copulation was sufficient to fertilize all the eggs of a female. Long copulations should therefore have other functions than securing the necessary amount of sperm for fertilization. We also found that neither the time until egg production after copulation, nor offspring size was affected by copulation duration. This suggests the lack of transfer of ejaculatory substances that would either stimulate the egg sac formation or increase the size of the spiderlings. We propose that prolonged copulations gain meaning in multiple mating situations and should play a role in sperm competition or other forms of sexual selection. The extra time may be used for copulatory courtship, or for the transfer of surplus sperm or other substances to manipulate the female’s willingness to copulate with other males, or to use sperm from them. These hypotheses remain to be tested in multiple mating experiments.

**Keywords:** Sperm transfer, copulation duration, copulation pattern, sexual selection, wolf spider

Copulation time varies largely in spiders even between closely related species. In the family of wolf spiders many species copulate for just a few minutes, while others copulate for hours. In a survey 30 species of wolf spiders, Stratton et al. (1996) noted that *Arctosa littoralis* (Hentz 1844) copulated for the shortest time, 18 seconds, while *Schizocosa saltatrix* (Hentz 1844) represented the opposite extreme with more than 8 hours. Copulation duration may vary widely even among species within the same genus, e.g. a 20 fold difference was found between the shortest and longest copulating *Hogna* spp. (Stratton et al. 1996). Our own observations on Old World lycosid species showed similar variable patterns. In a pilot study, *Pardosa hortensis* (Thorell 1872) copulated for 20–30 minutes, while *Pardosa agrestis* (Westring 1861) took

on average six times longer to copulate (A. Szirányi unpubl. data).

Given the examples for both short and long copulations, the question arises: what is the function of long copulation duration in wolf spiders, and in particular in the wolf spider, *Pardosa agrestis*? We chose to study *P. agrestis*, because it typically exhibits long copulation, and as the most abundant agrobiont spider in Central European arable fields (Kiss & Samu 2000; Samu & Szinetár 2002), it is the primary model species of our research group. The species builds no retreat and it hunts actively on the ground during the day (Samu et al. 2003). *Pardosa agrestis* has two reproductive peaks, with mating periods mostly in May and in July-early August (Samu et al. 1998). So far, we could not establish whether females remate in nature, but they do so in the labo-



ratory (Kiss 2003). Egg sacs are produced 2–3 weeks after copulation, and they are carried by the female for an average of 3 weeks until hatching.

The main function of copulation is sperm transfer, which may take a long or a short time. Long copulation duration might be necessary for complete fertilization, if sperm transfer is slow. Slow sperm transfer could be a common phylogenetic constraint, however in a taxonomic group in which copulation duration varies widely, this can be ruled out. On the other hand, long copulation has to be evolutionarily maintained, because it is likely to be costly. The time spent copulating is energetically demanding (Watson & Lighton 1994), and it entails a loss of opportunity to copulate with other partners or to forage. In species in which copulation takes place without hiding in a refuge, like in *P. agrestis*, an elevated predation risk can also be expected (Krupa & Sih 1998). Long copulation might also expose the spiders to parasite infection (Scheffer 1992). Thus, lacking a phylogenetic explanation, and considering possible costs, we should look for the adaptive value of prolonged mating.

To find the possible adaptive value of prolonged copulation in *P. agrestis* we created a hypothesis framework, and tested it in single mating experiments where the copulations were interrupted to ensure predefined duration. Three different scenarios of time-use were constructed (Fig. 1). From each scenario, specific predictions can be formulated and tested.

We consider hypothesis A to be the null-scenario, in which sperm is transferred throughout the entire copulation time and it is all used for fertilization. In this scenario sperm transfer is insufficient if copulation time is limited which prevents the fertilization of all ova. Indeed, copulation duration is positively associated with sperm transfer in a number of arthropods (Dickinson 1986; Arnqvist & Danielsson 1999; Stålhandske 2001), but in other cases, like in the spider *Micrathena gracilis* (Walckenaer 1805), this relationship does not exist (Bukowski & Christenson 1997). A prediction from Hypothesis A is that shorter than natural copulation time would result in a reduced number of fertilized eggs and offspring. In the following hypotheses (B and C) the sperm transfer rate

## Hypothesis: Copulation pattern:

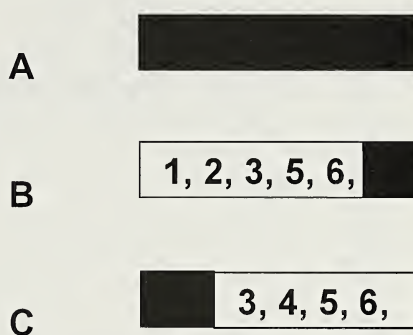


Figure 1.—Hypotheses concerning copulation pattern. There are two considered components to the pattern: 1. (shaded areas) periods when sperm used for fertilization is transferred; 2. (empty areas) periods when either no sperm is transferred or no such sperm that would be used for fertilization (= non-fertilizing period). Numbers indicate some possible functions of the no-transfer/non-fertilizing period: 1. removing earlier male sperm and/or plug; 2. assessing female virginity; 3. in-copula courtship; 4. transferring extra sperm; 5. transferring materials to accelerate oogenesis; 6. transferring nutritive materials (nuptial gift). See details in text; for further possible functions see Eberhard (1996).

does not limit fertilization, but rather the prolonged copulation duration is maintained by other factors.

With hypothesis B we propose the scenario that the sperm transfer is timed for the end of the copulation. In that case, the first part of the copulation then serves other purposes, such as copulatory courtship. Just as courtship influences female choice, copulatory courtship can influence female choice regarding postcopulation events. In spiders, sperm transfer and fertilization are well separated in time, and during the period between transfer and fertilization females may manipulate which male's sperm is used for fertilization via "cryptic female choice" (Watson & Lighton 1994; Eberhard 1997; Schäfer & Uhl 2002). In Linyphiidae the first part of copulation, the phase without sperm transfer, is often referred to as pseudo-copulation (Helsdingen 1965). Males are able to distinguish virgin from non-virgin females during courtship and pseudo-copulation (Robinson 1982; Suter 1990). This phase of mating can also be used to remove the sperm (Schäfer & Uhl 2002) placed by a pre-

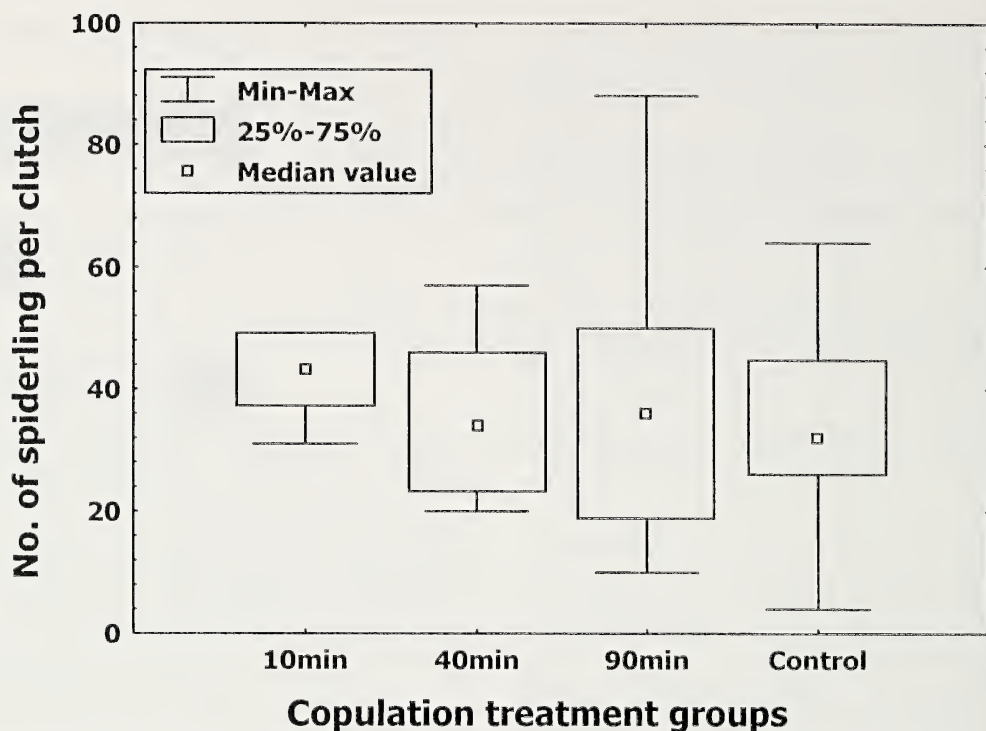


Figure 2.—The number of spiderlings in a clutch as a function of copulation length.

vious mate in the female's genital tract. From Hypothesis B we can predict that copulation interrupted early will result in no sperm transfer, and consequently in no hatched offspring from the egg sacs later.

In Hypothesis C the volume of sperm necessary to fertilize the eggs is transferred at the beginning of copulation and the rest of the time is used for other activities. The remaining copulatory time can, similar to Hypothesis B, serve the purpose of copulatory courtship, or it may simply engage the female long enough, so that competing mates will have reduced chances of copulation (mate guarding). Another possibility is that these activities decrease female receptiveness to the sexual advances of other males (Eberhard 1996). Having transferred the necessary amount of sperm to fertilize all eggs, sperm transfer might continue. Surplus sperm might be advantageous if females mate multiple times, because then a greater volume of sperm can be used in numerical sperm competition (Elgar 1998). In some species after sperm transmission, males create mating plugs in the genital opening of the female to prevent further copulations (Masumoto 1993; Knoflach 1998). Males may

transfer substances to the female that facilitate rapid oviposition, thus leaving less time for the female to meet and mate with competing males prior to egg deposition (Yamaoka & Hirao 1977). Nutritive substances might also be transferred to the female genital tracts (Suter & Parkhill 1990), which increase offspring size, thus increasing parental fitness. Hypothesis C predicts that in a single copulation, the female's reproductive output should remain unchanged after the first part of copulation. On the other hand, the various possible functions of the remaining copulation time generate additional predictions for offspring size and period until oviposition.

We interrupted copulations after three different time intervals to distinguish between the above hypotheses. Here we report the relationship between the artificially set copulation duration and reproductive output. These experiments show which of the originally proposed hypotheses are rejected or supported and cast some light on the function of various phases of copulation.

#### METHODS

The experiment was conducted from April to September, 1998 at the Plant Protection In-



stitute of the Hungarian Academy of Sciences (near Budapest). *Pardosa* individuals were hand-collected in juvenile or subadult stages in April to ensure virgin adults for the experiment. Animals were kept separately in the laboratory, where they were reared to adulthood under standard conditions (25 °C, long daylight (L:D = 16:8), and *Drosophila melanogaster* ad libitum was provided as food). Basic rearing conditions are explained in Kiss & Samu (2002).

#### Interrupted copulation experiment.—

Following maturation, adult males and females were divided randomly into four groups. Pairs from each group were put together in 17 cm diameter Petri dishes, and the occurrence of copulation was monitored. In the first three treatment groups copulation was interrupted after 10 min ( $n = 16$ ), 40 min ( $n = 22$ ), and 90 min ( $n = 16$ ) respectively. The pairs in the fourth group (Control) were left undisturbed until they finished copulation ( $n = 20$ ). To establish the distribution of uninterrupted copulation duration, additional observations on copulation length were performed ( $n = 42$ ), in which the reproductive consequences were not observed.

After copulation, females were kept in the laboratory under the conditions presented above. We recorded the time between copulation and oviposition (in some cases, exact time of oviposition could not be recorded, which resulted in smaller sample sizes for that variable:  $n_{10\text{min}} = 9$ ,  $n_{40\text{min}} = 7$ ,  $n_{90\text{min}} = 7$ ,  $n_{\text{control}} = 8$ ); whether females abandoned or consumed their egg sac, and whether the hatching was successful. We calculated the ratio of abandoned egg sacs as the number of egg sacs abandoned in an interruption treatment / all egg sacs produced in the given treatment. We monitored mothers with egg sacs for hatching daily. If hatching was successful we counted the number of offspring (thus offspring number counts are based only on successful hatches), and placed a sample of 10 spiderlings into 70% ethanol. Later we estimated the prosomal area ( $\text{length}_{\text{max}} \times \text{width}_{\text{max}}$ ) on this random sample of ten spiderlings of each brood using scaled digital pictures. For the size measurement, we chose to measure the prosoma because it is less prone to the current feeding status (e.g. cannibalizing a littermate) of the spiderling. Voucher specimens were deposited

in the public collection of the Plant Protection Institute, Hungarian Academy of Sciences.

## RESULTS

The duration of spontaneously ended (uninterrupted) copulation events was over 2.5 hours (mean = 165.7 min; S.D. = 53.6; range = 90–319 min). Interruption of the copulation did not affect the number of offspring from hatched egg sacs (Fig. 2; ANOVA:  $F_{3,40} = 0.46$ ,  $P = 0.71$ ; homogeneity of variances assumption tested by Levene's Test:  $F_{3,40} = 2.13$ ,  $P = 0.11$ ). The prosomal area of the offspring did not differ significantly between copulation duration treatments with the effect of mothers nested within treatment (ANOVA, main treatment effect:  $F_{3,478} = 0.35$ ,  $P = 0.79$ ). However, the effect of mothers on offspring size was highly significant (ANOVA, effect of mothers nested within treatment:  $F_{38,478} = 6.11$ ,  $P < 0.0001$ ). The time between copulation and egg sac production was not significantly different among the treatments (overall mean = 20.6 days, S.D. = 3.88, ANOVA:  $F_{3,27} = 0.10$ ,  $P = 0.96$ ). Egg sac abandonment, on the other hand, occurred unevenly among the treatments (test of homogeneity:  $\chi^2 = 8.62$ ; d.f. = 73,  $P = 0.035$ ). As Fig. 3 illustrates, abandonment ratio was particularly high (0.56) in the 10 min interruption group, significantly higher than in the other treatments (10 minutes vs. other treatments lumped, Fisher's Exact Test:  $n = 74$ ,  $P = 0.01$ ). Among the longer than 10 minutes copulation treatments and the control group, the abandonment ratio was equally low (on average 0.2, test of homogeneity:  $\chi^2 = 1.01$ ; d.f. = 57,  $P = 0.6$ ).

## DISCUSSION

In the present study, we wanted to establish the pattern of sperm transfer during the long copulation of *P. agrestis*. Our first hypothesis, Hypothesis A (Fig. 1), was that copulation takes longer because sperm transfer rate is slow. This hypothesis can be rejected, because the interruption experiment demonstrated that sperm transferred even in the first 10 minutes of copulation can be sufficient to fertilize all eggs of a female; offspring numbers were independent of copulation treatments. These results also cause Hypothesis B to be rejected, because this hypothesis predicted zero reproductive output for short copulation treatments.



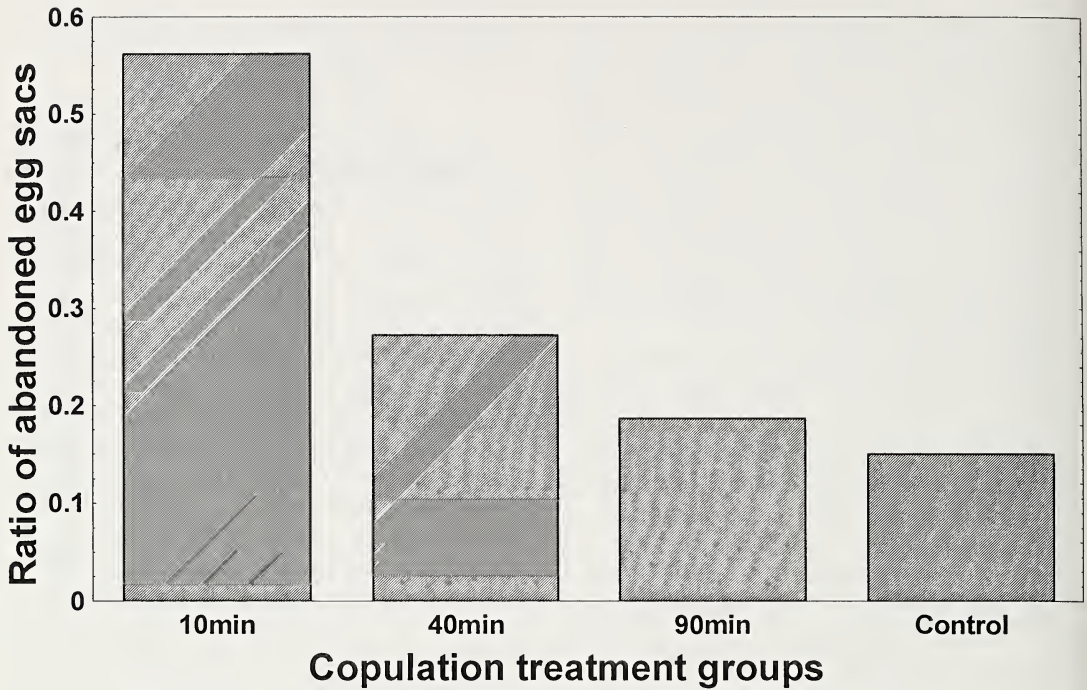


Figure 3.—The ratio of abandoned egg sacs in the copulation duration treatments.

The interruption results are consistent only with Hypothesis C, which proposes a copulation pattern in which the transfer of sperm needed to fertilize the eggs takes place within a short period at the beginning of the copulation.

However, egg sac abandonment was significantly more frequent in the 10 min copulation treatment than in any of the other treatments. Since egg sacs are abandoned when they are sterile (Kiss 2003), this suggests that there is variability in the first 10 minutes of mating. That is, in some cases, during the first 10 minutes enough sperm was transferred to fertilize all eggs of the future egg sac, while in other cases, no sperm was transferred and the egg sacs were sterile. We can speculate that this can happen if the event of sperm transfer is fast, even compared to the 10 min time scale. Sperm transfer seemed to occur with c. 50% probability during the first 10 min, and with near certainty during the first 40 min of the copulation. Since we had no direct observation on the ratio of sterile and fertilized eggs in the abandoned egg sacs, we can only infer from previous observations that they were likely to be sterile. We note a 20% baseline abandonment which occurred in all longer in-

terruption treatments, including the control, and which could be either a natural phenomenon, or an artifact caused by the experimental situation. A similar phenomenon has been described in the salticid *Phidippus johnsoni* (Peckham & Peckham 1883), in which copulation duration also had an all-or-none effect on fertility, with short copulations more frequently resulting in the 'none' outcome, and long copulations more frequently resulting in a fully fertilized clutch (an 'all' outcome), whereas no half-sized clutches occurring (Jackson 1980). Jackson (1980) did not provide an alternative explanation to the quick release of a large amount of sperm, with an increasing probability over time.

Thus, the basic copulation pattern of *P. agrestis* corresponds to Hypothesis C: rapid transfer of an amount of sperm that is enough to fertilize all eggs takes place at some point during the first part of the copulation, while the final phase, which is the longer portion of time spent in copula, does not serve the direct purpose of transferring sperm to fertilize the eggs. Given this pattern, the question remains concerning the function of the final phase of copulation. In Fig.1 we list a number of such possible functions. Of these, some can be ex-



cluded based on the present experiment. Since spiderlings were of equal size irrespective of copulation duration, there is no evidence that the male transferred any nutrients during the final phase of the copulation in order to increase parental fitness through offspring size (Suter & Parkhill 1990; Walker et al. 2003). The transfer of materials that could accelerate oogenesis can also be ruled out on the basis of similar egg sac formation times across the copulation duration treatments. We did not find any evidence for the presence of a mating plug. Although, we could rule out a number of proposed functions for the final phase of the copulation, several other functions still remain possible. If surplus sperm are transferred, the sperm could be used to out-compete the sperm of other possible mates. The final phase of copulation may also serve as copulatory courtship or as mate guarding. These functions are not mutually exclusive, and any combination of them is possible.

To summarize, the copulation pattern established for *P. agrestis* seems to be paradoxical in a single mating situation, because much shorter copulations are sufficient to result in full fertilization. Any possible function of a long copulation that was not experimentally excluded here seems to be related to male-male competition and/or female choice, and gains meaning only in a multiple mating situation. Therefore, we tentatively conclude that prolonged copulation is a sexually selected trait in *P. agrestis*. To establish the functional details and exact adaptive advantages, multiple mating studies are needed.

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## LARVAL CHAETOTAXY IN WOLF SPIDERS (ARANEAE, LYCOSIDAE): SYSTEMATIC INSIGHTS AT THE SUBFAMILY LEVEL

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**ABSTRACT.** Studies into the systematics of wolf spiders have mainly employed morphological characters of adult spiders, in particular features of the male and female genitalia, and more recently mitochondrial DNA sequence data. However, there is still no established phylogenetic framework for the Lycosidae, even at the subfamily level. This study uses a novel morphological character set, the chaetotaxy of lycosid larvae (presence and arrangement of setae and slit organs), to infer systematic information on seven species of wolf spiders that are currently listed in three subfamilies: Lycosinae [*Alopecosa pulverulenta* (Clerck 1757), *Hogna antelucana* (Montgomery 1904), *Rabidosa rabida* (Walckenaer 1837), *Trochosa ruricola* (DeGeer 1778)], Piratinae [*Hygrolycosa rubrofasciata* (Ohlert 1865), *Pirata hygrophilus* (Clerck 1757)], and Sosippinae (*Sosippus californicus* Simon 1898). Cheliceral and tarsal (legs I and II) chaetotaxic patterns of the first postembryo showed equivalent chaetotaxic complexes amongst all species but revealed considerable differences between representatives of the three subfamilies. *Sosippus californicus* showed the most complex pattern and *P. piraticus* the most reduced arrangement. In addition, it casts doubt on the previous listings of *H. rubrofasciata* in either the Lycosinae or Piratinae, as its chaetotaxic setae arrangement was more similar to *S. californicus* than to any other species investigated here.

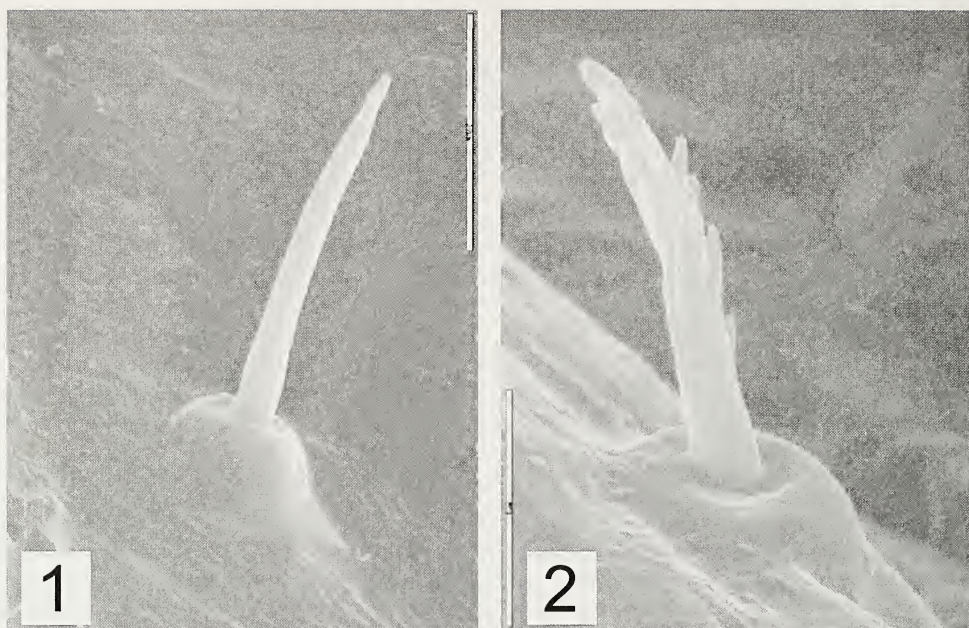
**Keywords:** Larval stages, chaetotaxic complex, Lycosinae, Piratinae, Sosippinae

Chaetotaxy, the presence and arrangement of setae and other sensory structures on the integument of arthropods, has been widely used for systematic and taxonomic studies in a variety of groups, including insects (e.g. Alarie & Watts 2004) and arachnids such as mites (Tuzovsky 1987; Griffith et al. 1990) and pseudoscorpions (e.g. Chamberlin 1931; Harvey 1992). In contrast, investigations into the chaetotaxy of spiders are comparatively rare and have focused mainly on trichobothrial patterns. These have been argued to be a suitable feature in higher level systematics (Lehtinen 1980; Scioscia 1992). They may also serve as an important tool in identification at the species level. For example, the position of the metatarsal trichobothrium has been used as an essential character in the identification of central European Micryphantinae Bertkau 1872 (Wiehle 1960; Heimer & Nentwig 1990).

There is a considerable difference between the chaetotaxic pattern of immature and adult

arthropods and larval chaetotaxy has been argued to represent an excellent character set for systematic studies (Pomorski 1996). Larval morphology is of particular interest in holometabolic insects such as beetles (Kilian 1998; Borowiec & Świętojańska 2003) and butterflies (Kitching 1984, 1985) as different expressions of the same genotype can complement the morphological characters of adults (Alarie & Watts 2004; Grebennikov 2004; Ashe 2005). However, larval chaetotaxy has also been useful in phylogenetic and taxonomic studies of arthropods with gradual larval development such as springtails, mites and pseudoscorpions (Nayrolles & Betsch 1993; Pomorski 1996; Griffith et al. 1990; Harvey 1992). Early stages of development may last for only a short period of time, which in many cases eliminates the development of distinct adaptive traits. In addition, the morphology of juveniles is less variable and complex than that of adults (Pomorski 1996).





Figures 1, 2.—Larval setae of wolf spiders. 1. Seta form [position: apical/etc leg/chelicera etc] of [species]; 2. Serrated seta from [position: apical/etc., leg/chelicera etc.] of [species]. Scale bar: 10  $\mu\text{m}$  (Fig. 1), 5  $\mu\text{m}$  (Fig. 2).

Studies on chaetotaxic structures in immature spiders are rare and initially focused on trichobothrial patterns (Emerit 1964). A recent study of the linyphiid spider *Bathyphanthes eumenis* (L. Koch 1879) included all sensory structures of the protonymph and showed that the arrangement of sensory organs such as setae, trichobothria and slit organs was constant in all examined specimens and may have the potential to serve in the identification of spiders at the generic and species level (Rybak & Pomorski 2003). The nomenclature of the chaetotaxic patterns developed for *B. eumenis* was subsequently used in a detailed comparative study including the wolf spider *Trochosa ruricola* (DeGeer 1778) (Lycosidae) (Rybak & Tomasiewicz 2005). Although this study showed considerable differences in chaetotaxic pattern between both species, some body parts showed very similar setae distribution, which suggested homology for a large number of chaetotaxic complexes.

Despite recent investigations into the systematics of wolf spiders, there is still no accepted phylogenetic framework for the Lycosidae, even at the subfamily level (e.g. Dondale 1986; Zyuzin 1993; Vink et al. 2002). This problem can be attributed to a lack of well-

defined morphological characters that could classify and separate particular genera and subfamilies. However, there appears to be a consensus that web-building wolf spiders, such as the genera *Sosippus* Simon 1888 (sheet-web) and *Pirata* Sundevall 1833 (tube-shaped retreat) represent more ancient evolutionary lines in comparison to genera within the Lycosinae Simon 1898 (*Trochosa* C.L. Koch 1847, *Alopecosa* Simon 1885, *Rabidosa* Roewer 1960 and *Hogna* Simon 1885) that are considered representatives of more recent evolutionary lineages (Dondale 1986; Zehethofer & Sturmbauer 1998; Vink et al. 2002).

The genus *Hygrolycosa* Dahl 1908 was formerly placed in the Lycosinae along with, amongst others, *Alopecosa*, *Hogna* and *Trochosa* (Dondale 1986). However, more recently, it was listed in a separate subfamily, Piratinae Zyuzin 1993, based on the shape and location of the embolus and the functional conductor in the male pedipalp (Zyuzin 1993). Current molecular evidence suggests that *Hygrolycosa* is a sister taxon to *Aulonia albimana* (Walckenaer 1805) in a clade that also includes *Pirata*, *Venonia* Thorell 1894 (Venoniinae Lehtinen & Hippa 1979) and *Xeroly-*



Table 1.—Nomenclature of chaetotaxic complexes on the larval integuments of *A. pulverulenta*, *H. antelucana*, *H. rubrofasciata*, *P. hygrophilus*, *R. rabida*, *S. californicus* and *T. ruricola*.

Abbreviation	Chaetotaxic complex	Illustrations
Chelicerae		
Ch <sub>DA</sub>	dorsal apical complex	Figs. 1–4
Ch <sub>DM</sub>	dorsal median complex	Figs. 1–4
Ch <sub>VAM</sub>	ventral apico-median complex	Figs. 5–8
Ch <sub>VM</sub>	ventral median complex	Figs. 7–8
Tarsi I and II		
T <sub>DA</sub>	dorsal apical complex	Fig. 9
T <sub>DAI</sub> , T <sub>DAII</sub> ...	first, second, . . . dorsal apical complex	Figs. 10–11
T <sub>DM</sub>	dorsal median complex	Fig. 9
T <sub>DMI</sub> , T <sub>DMII</sub> ...	first, second, . . . dorsal median complex	Figs. 10–13
T <sub>DP</sub>	dorsal proximal complex	Figs. 10–13
T <sub>VAI</sub> , T <sub>VAII</sub> ...	first, second, . . . ventral apical complex	Figs. 12–14
T <sub>VM</sub>	ventral median complex	Fig. 12
T <sub>VMI</sub> , T <sub>VMII</sub> ...	first, second, . . . ventral medial complex	Figs. 13–14
T <sub>VP</sub>	ventral proximal complex	Figs. 13–14

*cosa* Dahl 1908 (Evippinae Zyuzin 1985) (N. Murphy et al. in press).

The main objective of this study was to evaluate the significance of larval chaetotaxic patterns for systematic analyses in wolf spiders. More specifically, we used the ambiguous subfamily placement of *H. rubrofasciata* to assess its previous listings in either the Lycosinae or Piratinae by including representatives of these subfamilies in our comparative analysis.

METHODS

We analyzed the larval stages of seven species of wolf spiders currently listed in three different subfamilies: Lycosinae [*Alopecosa pulverulenta* (Clerck 1757), *Hogna antelucana* (Montgomery 1904), *Rabidosa rabida* (Walckenaer 1837), and *Trochosa ruricola* (DeGeer 1778)], Piratinae [*Hygrolycosa rubrofasciata* and *Pirata hygrophilus* (Clerck 1757)], and Sosippinae [*Sosippus californicus* Simon 1898]. We obtained immature stages through laboratory colonies (*T. ruricola*, *A. pulverulenta*, *H. rubrofasciata* and *P. hygrophilus*) or loan and donation of material from overseas collections (*H. antelucana*, *R. rabida* and *S. californicus*).

Overall, we studied 64 specimens of *T. ruricola*, 10 specimens each of *H. rubrofasciata* and *P. hygrophilus* and 5 specimens each of *A. pulverulenta*, *H. antelucana*, *R. rabida*, and *S. californicus*. There was no intraspecific var-

iation in regard to the number of structures within chaetotaxic complexes, which allowed analysis of data without statistical consideration of variation.

Specimens were transferred to 5% KOH and cleared in distilled water. Subsequently, they were placed in chloramphenol and mounted in Swan medium (20 g distilled water, 60 g chloral hydrate, 15 g gum arabic, 3 g glucose, 2 g glacial acetic acid). All slides were examined under a phase contrast microscope (Nikon Eclipse E 600) with a drawing attachment. Scanning electron microscope (SEM) photographs were taken with a JEOL JSM-5800 LV at 15kV after spray-coating the specimen with gold. Voucher specimens of the species examined were lodged at the Museum of Natural History, Wrocław (*A. pulverulenta*, *P. hygrophilus*, *H. rubrofasciata*) and the California Academy of Sciences, San Francisco (*H. antelucana*, *R. rabida*, *S. californicus*).

**Larval stages.**—We investigated the first immature stage that possesses chaetotaxic structures on the integument, i.e. the first postembryo. These young spiders develop inside the egg-sac followed by the protonymph, which abandons the egg-sac (Vachon 1957). Vachon (1957) proposed the term ‘larva’ for the first postembryo, which corresponds to ‘stage D’ (Holm 1940), ‘préjuvenilé (Ji 1)’ (Canard 1987), ‘larva “setose stage”’ (Hallas 1988), and ‘IV instar’ (Galiano 1991). Con-

sequently, all references to 'larvae' or 'larval' in this study refer to the first postembryo.

**Chaetotaxic structures.**—Although numerous chaetotaxic structures such as spines, trichobothria, proprioceptors in the form of hair plates, and chemoreceptors in the form of tarsal organs, and taste hairs exist in spiders (Foelix 1996; Rybak & Pomorski 2003), this study deals with setae and slit organs because only these structures were observed on the larval integument. In adult spiders, setae are triply innervated hair-like structures that serve purely mechanical tasks (tactile receptors). They consist of a long exocuticular shaft of variable shape (including serrated and plumose), which is suspended in a slipper-shaped socket in which it can move (Rybak & Pomorski 2003). In contrast, spines are rigid structures that are regarded as hemolymph pressure receptors (Foelix & Chu-Wang 1973). In immature spiders, it is difficult to distinguish between spines and setae as the socket and the setae are generally not fully developed (Figs. 1, 2), although different types of setae may exist (Bond 1994). Consequently, within the scope of our study, we do not differentiate between setae and spines. Slit organs occur both in adult and larval spiders. They sense mechanical stress in the exoskeleton caused by vibrations, gravity or the spider's own movement and occur singly ('slit sensillae') or in groups where slits run parallel to each other ('lyriform organs') (Foelix 1996). In this study, the chaetotaxic structures on larval chelicerae and tarsi were grouped into distinct complexes. The nomenclature of these complexes follows Rybak & Pomorski (2003) and Tomasiewicz & Rybak (2005) (see also Table 1).

## RESULTS

There were considerable differences in the number of chaetotaxic structures on the larval bodies of the investigated species, which allowed separating them into two main groups (Tables 2 & 3). While *A. pulverulenta*, *H. antelucana*, *P. hygrophilus*, *R. rabida* and *T. ruricola* possessed chaetotaxic structures only on the chelicerae, labium, maxillae, legs and pedipalps, *H. rubrofasciata* and *S. californicus* exhibited chaetotaxy on all body parts including sternum, carapace, abdomen and spinnerets. Chelicerae and the tarsi of legs I and II showed distinct chaetotaxic patterns, which

allowed a comparison between species and genera. These structures were most complex in *S. californicus* (Figs. 6, 10, 13, 16) and *H. rubrofasciata* (Figs. 5, 9, 12, 15) and most reduced in *P. piraticus* (Figs. 3, 7, 11, 14).

**Chelicerae dorsal.**—All species possessed the apical complex  $Ch_{DA}$ . The number of setae within this complex differed between *P. hygrophilus* (four setae; Fig. 3), a group comprising *T. ruricola*, *A. pulverulenta*, *R. rabida*, and *H. antelucana* (seven setae; Fig. 4) and a group with *H. rubrofasciata* and *S. californicus* (10 setae; Figs. 5, 6). *Hygrolycosa rubrofasciata* and *S. californicus* had an additional median complex  $Ch_{DM}$  that consisted of three setae, which were long in *S. californicus* and very short in *H. rubrofasciata*. All species had one slit sensilla in the median section of the chelicerae and two slit sensillae apically (Figs. 3–6).

**Chelicerae ventral.**—All species showed an apico-median complex  $Ch_{VAM}$  that consisted of one or two setae in *P. hygrophilus* (Fig. 7), and four setae in all other species (Figs. 8–10). *Hygrolycosa rubrofasciata* (Fig. 9) and *S. californicus* (Fig. 10) possessed a further structure  $Ch_{VM}$ , consisting of a single seta in *H. rubrofasciata* and two setae in *S. californicus*. The latter species showed an additional apical seta  $Ch_{VA}$  that did not exist in any of the other lycosids. All species possessed two slit sensillae apically (Figs. 7–10).

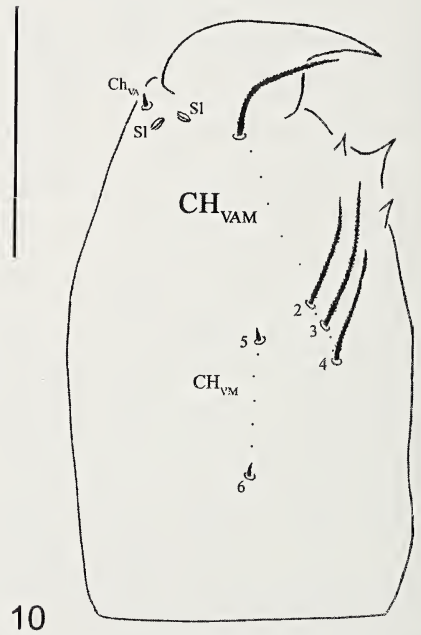
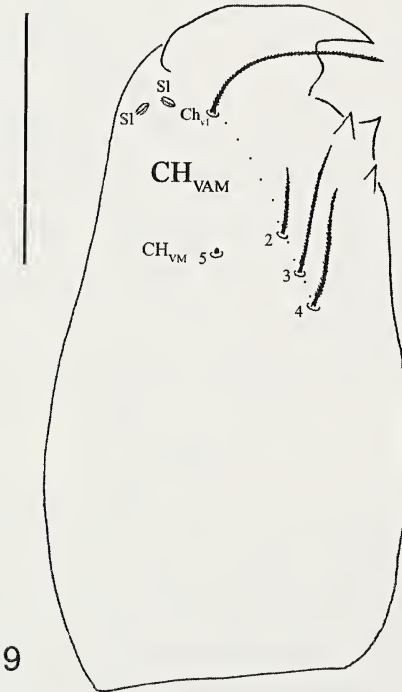
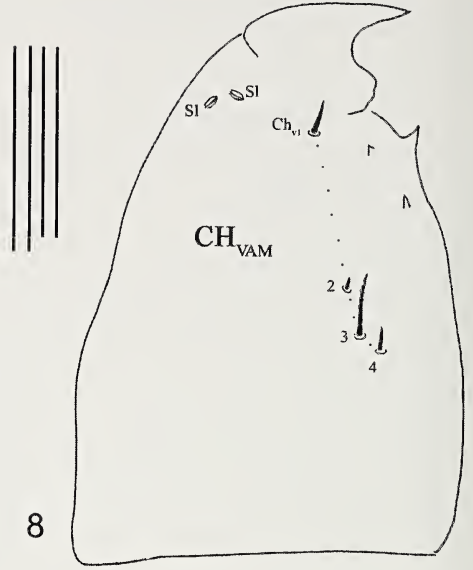
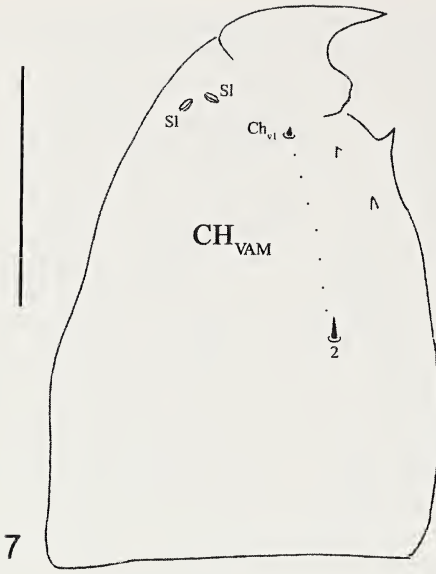
**Tarsi of legs I and II dorsal.**—All species examined showed two similar complexes,  $T_{DA}$  and  $T_{DM}$  in *T. ruricola*, *H. antelucana*, *R. rabida*, *A. pulverulenta*, and *P. hygrophilus* (Fig. 11), corresponding to  $T_{DAIII}$  and  $T_{DMIV}$  in *H. rubrofasciata* (Fig. 12) and  $T_{DAII}$  and  $T_{DMIV}$  in *S. californicus* (Fig. 13). *Hygrolycosa rubrofasciata* (Fig. 12) and *S. californicus* (Fig. 13) showed seven more complexes in which the apical ones had a larger number of setae in *S. californicus*. All lycosids showed slit sensillae located laterally in the median part of the tarsi (Figs. 11–13).

**Tarsi of legs I and II ventral.**—All species showed three identical complexes,  $T_{VAI}$ ,  $T_{VAII}$ , and  $T_{VM}$  in *T. ruricola*, *H. antelucana*, *A. pulverulenta* and *P. hygrophilus* (Fig. 14), corresponding to  $T_{VAI}$ ,  $T_{VAIII}$ , and  $T_{VMI}$  in *H. rubrofasciata* and *S. californicus* (Figs. 15–16). The complex  $T_{VMI}$  consisted of three setae in *H. rubrofasciata* (Fig. 15) (as the equivalent complex  $T_{VM}$  in the other above-men-





Figures 3-6.—Chaetotaxic pattern on dorsal side of the chelicerae in wolf spider larvae: 3. *Pirata hygrophilus*; 4. *Alopecosa pulverulenta*, *Hogna antelucana*, *Trochosa ruricola*, *Rabidosa rabida*; 5. *Hygrolycosa rubrofasciata*; 6. *Sosippus californicus*. Scale bar: 0.1 mm. Multiple scale bars in Fig. 4 reflect the comparative scale of the species in the given sequence.



Figures 7–10.—Chaetotaxic pattern on ventral side of the chelicerae in wolf spider larvae: 7. *Pirata hygrophilus*; 8. *Alopocosa pulverulenta*, *Hogna antelucana*, *Trochosa ruricola*, *Rabidosa rabida*; 9. *Hygrolycosa rubrofasciata*; 10. *Sosippus californicus*. Scale bar: 0.1 mm. Multiple scale bars in Fig. 8 reflect the comparative scale of the species in the given sequence.



tioned lycosids), but included four setae in *S. californicus* (Fig. 16). *Sosippus californicus* and *H. rubrofasciata* showed six additional complexes ( $T_{VAII}$ ,  $T_{VC}$ ,  $T_{VMII}$ ,  $T_{VMIII}$ ,  $T_{VMIV}$ ,  $T_{VP}$  in *H. rubrofasciata* and  $T_{VAII}$ ,  $T_{VMII}$ ,  $T_{VMIII}$ ,  $T_{VMIV}$ ,  $T_{VMV}$ ,  $T_{VP}$  in *S. californicus* (Figs. 15, 16). Although these two species showed the most similar chaetotaxic patterns, there are complexes ( $T_{VMIV}$ ,  $T_{VC}$  in *H. rubrofasciata* and  $T_{VMIV}$ ,  $T_{VMV}$  in *S. californicus*) (Figs. 15, 16) among which it is difficult to establish homology. Both species showed slit sensillae situated medially near the apical part of the tarsi, which were absent in all other species (Figs. 14–16).

## DISCUSSION

Our analysis of chaetotaxic patterns in wolf spiders showed distinct and regular complexes for all species examined. These complexes appear to be similar to the arrangement in other spider families such as the Linyphiidae (Rybak & Pomorski 2003), which suggests that larval chaetotaxy may serve as a very useful character set in systematic studies if homologies can be established on a higher taxonomic level. However, there was no difference of chaetotaxic patterns among any of the species currently included in the subfamily Lycosinae. In contrast to other arthropods, in particular insects (e.g. Deruaz et al. 1991; Alarie & Watts 2004), larval chaetotaxy does not seem to be suitable for the identification of taxa below subfamily level in wolf spiders.

There were significant differences in the number of complexes of cheliceral and tarsal setae and the number and size within these complexes. *Sosippus californicus* showed the most complex pattern along with *H. rubrofasciata* that differed only in the absence of two setae on the ventral side of the chelicerae, the absence of the complex equivalent to  $T_{VMIV}$  in *S. californicus*, and a reduction in the number of setae in the apical and proximal complexes of the tarsi. On the other hand, all four species of Lycosinae and *P. piraticus* showed very similar setal arrangements (Table 2). Here, chaetotaxy was heavily reduced in comparison to *Sosippus* and *Hygrolycosa*, in particular in regard to the tarsal setae. *Pirata piraticus* had the lowest number of setae as complex  $CH_{DA}$  and  $CH_{VM}$  had two setae less each than the equivalent complexes in the Lycosinae. This separation into two major groups, supported

by the overall distribution of chaetotaxic complexes on the bodies of the spiders (Table 3), does not reflect current phylogenetic hypotheses for wolf spiders. Morphological (Dondale 1986) and molecular (Zehethofer & Sturmbauer 1998; Vink et al. 2002; Murphy et al. in press) phylogenies consider the Lycosinae as the most derived lineage of wolf spiders, whereas the Piratinae and Sosippinae are thought to represent more basal evolutionary lines.

Although we included a wide range of taxa from different currently recognized subfamilies our study is ambiguous in regards to the plesiomorphic condition for larval chaetotaxic structures. Both *Pirata* and the sheet-web building *Sosippus* are thought to represent basal lineages in the evolution of wolf spiders but they differ considerably in their larval chaetotaxy. Preliminary studies on the chaetotaxy of *Pisaura mirabilis* (Clerck 1757) representing the Pisauridae, a putative sister taxon of the Lycosidae (Dondale 1986; Griswold 1993), show considerably reduced chaetotaxic patterns (Tomasiewicz unpub. data) supporting *P. hygrophilus* to display the plesiomorphic state. In this case, and in combination with current phylogenetic hypotheses (Murphy et al. in press), an increase in chaetotaxic structures has evolved twice within our sampled taxa, in *Sosippus* and *Hygrolycosa*.

The chaetotaxic pattern of *H. rubrofasciata* differs considerably from all other lycosine and piratinae species examined, the two subfamilies where it was previously listed (Dondale 1986; Zyuzin 1993) and our study suggests an alternative placement within the Sosippinae. However, current molecular data place *H. rubrofasciata* in a basal lineage within in the Lycosidae, close to the Venoniinae, Piratinae and Evippinae (Murphy et al. in press), providing support for Zyuzin's (1993) placement of the genus and at the same time rejecting chaetotaxic patterns as informative for the subfamilial placement of *Hygrolycosa*.

This preliminary study shows that larval chaetotaxy may provide some additional morphological evidence that bears phylogenetic information in spiders although some discrepancies with common tenets of current phylogenetic hypotheses in wolf spiders exist. It is not possible to distinguish species or even





Table 2.—Number of setae per chaetotaxic complex on the chelicerae and tarsi of leg II and III of *A. pulverulenta*, *H. antelucana*, *H. rubrofasciata*, *P. hygrophilus*, *R. rabida*, *S. californicus* and *T. ruricola*.

	<i>A. pulverulenta</i> <i>H. antelucana</i>			
	<i>P. hygrophilus</i>	<i>R. rabida</i> , <i>T. ruricola</i>	<i>H. rubrofasciata</i>	<i>S. californicus</i>
Ch <sub>DA</sub>	7	7	10	10
Ch <sub>DM</sub>	—	—	3	3
Ch <sub>VAM</sub>	2	4	4	4
Ch <sub>VM</sub>	—	—	1	2
T <sub>DA</sub>	3	3	—	—
T <sub>DAI</sub>	—	—	5	5
T <sub>DAII</sub>	—	—	2	3
T <sub>DAIII</sub>	—	—	3	2
T <sub>DM</sub>	2	2	—	—
T <sub>DMI</sub>	—	—	4	4
T <sub>DMII</sub>	—	—	3	3
T <sub>DMIV</sub>	—	—	2	2
T <sub>DMV</sub>	—	—	2	2
T <sub>DP</sub>	—	—	2	2
T <sub>VAI</sub>	2	2	2	2
T <sub>VAII</sub>	—	—	4	4
T <sub>VAIII</sub>	—	—	3	3
T <sub>VM</sub>	3	3	—	—
T <sub>VMI</sub>	—	—	3	4
T <sub>VMI</sub>	—	—	4	5
T <sub>VMI</sub>	—	—	3	2
T <sub>VMIV</sub>	—	—	4	3
T <sub>VMV</sub>	—	—	—	3
T <sub>VC</sub>	—	—	2	—
T <sub>VP</sub>	—	—	4	4

tain only a limited amount of information since a reduction of structures may have easily occurred in multiple evolutionary lines. Distinguishable morphological categories of setae exist in wolf spider larvae, for example smooth and serrated forms (Figs. 1, 2). Future research could explore an expanded character set and subsequently code it as morphological matrix for a phylogenetic analysis similar to some studies of insects (e.g., Alarie & Watts 2004; Ashe 2005). This could then be incorporated in an exhaustive morphological and molecular dataset for higher phylogenetic analysis in spiders.

The analysis of larval chaetotaxy may bear considerable importance in interpreting structures of mature spiders, in particular during character polarization as part of a phylogenetic analysis (ontogenetic criterion, see Hennig 1966; Nelson 1978; Mabee 2000). For example, the study of setal arrangement during postembryonic development has been helpful in determining the phylogenetic migration of

homological chelal trichobothria in pseudoscorpions (Harvey 1992) and the setal arrangement in astigmatid mites (Griffith et al. 1990).

Currently, it remains difficult to acquire larval material for morphological studies since larvae and juveniles are often discarded during the collection of spiders, and, if collected, the material may not represent a suitable developmental stage for comparative studies. However, if larval chaetotaxy can be established as an important morphological tool in phylogenetic studies of spiders, the collection and preservation of spider larvae may receive much stronger support.

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Table 3.—Presence of chaetotaxic structures on the larval bodies of *A. pulverulenta*, *H. antelucana*, *H. rubrofasciata*, *P. hygrophilus*, *R. rabida*, *S. californicus* and *T. ruricola*. sl – slit sensillae, ly – lyriform organs.

	<i>A. pulverulenta</i> <i>H. antelucana</i> , <i>P. hygrophilus</i> <i>R. rabida</i> , <i>T. ruricola</i>	<i>H. rubrofasciata</i> <i>S. californicus</i>
Chelicerae	setae, sl	setae, sl
Labium	setae	setae
Maxillae	setae	setae
Sternum	—	setae, sl
Carapace	—	setae
Pedipalps	setae, ly, sl	setae, ly, sl
Legs	setae, ly, sl	setae, ly, sl
Abdomen	—	setae
Spinnerets	—	setae

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## A REDESCRIPTION OF *PORRHOMMA CAVERNICOLA* KEYSERLING (ARANEAE, LINYPHIIDAE) WITH NOTES ON APPALACHIAN TROGLOBITES

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**ABSTRACT.** The Appalachian troglobite *Porrhomma cavernicola* (Keyserling 1886) is redescribed. *Porrhomma emertoni* Roewer 1942 is a junior synonym (new synonymy). An unusual stridulatory organ with the plectrum on trochanter II and the striae on coxa I is found in both sexes of this species. *Porrhomma cavernicola* is widespread in Appalachian caves. By contrast, Appalachian *Nesticus* (Nesticidae) troglobites tend to be highly endemic. This despite the fact that both groups of spiders are web-builders that may be found in the same caves. *Porrhomma cavernicola* is added to a previous phylogenetic analysis of linyphiid spiders. Implications of this analysis for the phylogenetic structure of linyphiid spiders is discussed.

**Keywords:** Dispersal, phylogeny, stridulatory organ, *Nesticus*, Nesticidae

There is a continuous gradation between epigean and troglobitic organisms. While a variety of spiders are known from cave entrances or can be found both in and out of caves, true troglobites complete their entire life cycle in caves. In the Appalachian region, true troglobites belong to the Linyphiidae, Nesticidae, Dictynidae and Leptonetidae (Barr 1961; Holsinger & Culver 1988; Gertsch 1992; Peck 1998). Dictynid and leptonetid troglobites in Appalachia are understudied and will not be discussed further here (see Miller 2005).

*Porrhomma cavernicola* (Keyserling 1886) is one of two linyphiid troglobites widespread and often syntopic in Appalachian caves. The other widespread linyphiid troglobite is *Phanetta subterranea* (Emerton 1875) (Fig. 1). *Anthrobia* are also widespread in Appalachian caves, although Miller (2005) has concluded that there are at least two troglobitic *Anthrobia* species instead of the one species previously recognized. Some other linyphiid troglobites have more restricted distributions (e.g., some *Islandiana* species, Holsinger & Culver 1988; Gertsch 1992; Peck 1998; also some

undescribed species, N. Dupérré, pers. comm.). Multiple linyphiid troglobite species can often be found in the same cave. By contrast, troglobitic species of *Nesticus* (Nesticidae) in Appalachian caves are never widespread, highly endemic, and rarely syntopic (Fig. 1; Gertsch 1984; Coyle & McGarity 1991; Hedin 1997b; Reeves 2000; Hedin & Dellinger 2005). About eight Appalachian *Nesticus* species appear to be troglobites (Gertsch 1984, 1992; Hedin 1997a; Hedin & Dellinger 2005). In both *Nesticus* (Hedin 1997a, b) and linyphiids, troglobitism seems to have occurred independently multiple times.

Widespread troglobites are the exception to the rule. Troglobites cannot normally survive long under surface conditions so dispersal between cave-islands across epigean seas must be rare (Barr 1967; Culver 1970, 1971, 1982; Barr & Holsinger 1985; Holsinger & Culver 1988). Thus widespread troglobites must either be a syndrome of multiple forms erroneously lumped into a single species by taxonomists, or genetically isolated populations that have not diverged because of insufficient time or low rates of change, or there must be some mechanism allowing gene flow between caves. Examination of specimens from across the range of *Porrhomma cavernicola* revealed no clear pattern of geographical variation that

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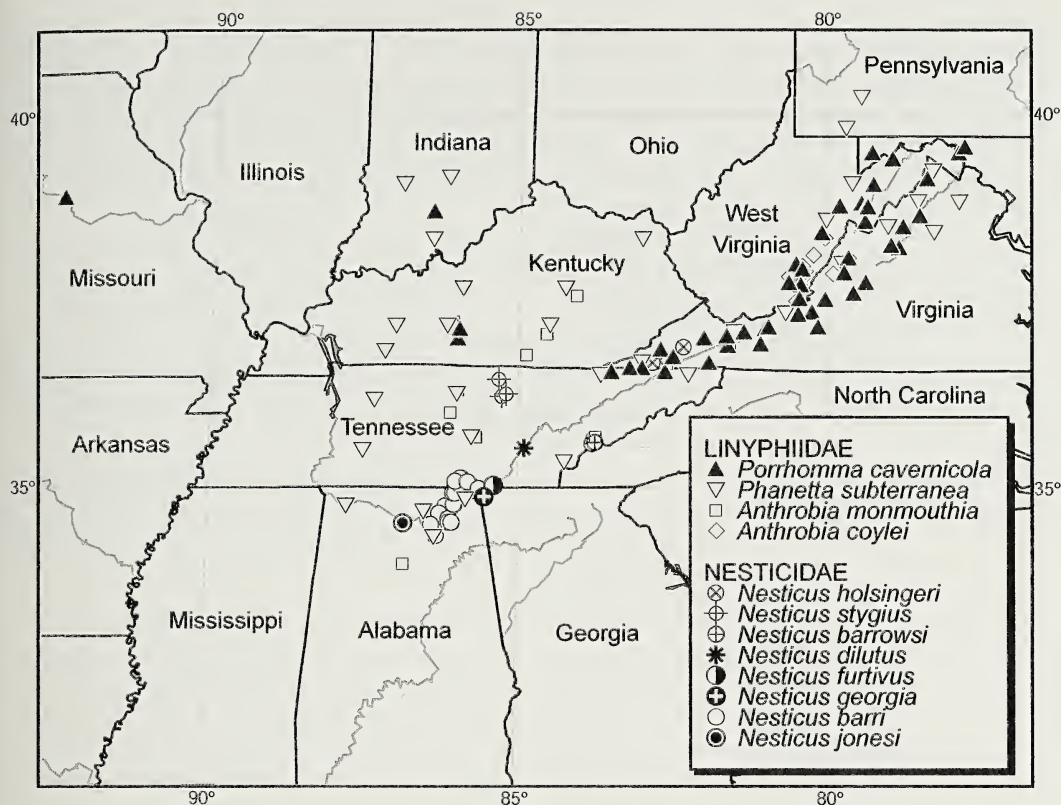


Figure 1.—Map showing distribution of nesticid and selected linyphiid troglobites in Appalachian caves. Records of *Phanetta subterranea* from Millidge (1984); of *Anthrobia monmouthia* and *Anthrobia coylei* from Miller (2005); of *Nesticus* species from Gertsch (1984) and Hedin (1997a, 1997b).

would suggest cryptic species (Figs. 2–4). This contrasts with the conclusion reached concerning troglobitic *Anthrobia*. *Anthrobia monmouthia* was previously considered a widespread Appalachian troglobite, but new work has provided diagnoses and descriptions for two distinct species that were previously confused under this name (Miller 2005). Efforts are underway to study the population genetics of widespread linyphiid troglobites in Appalachia to evaluate gene flow among caves.

## METHODS

Specimens were examined using a Leica MZ 16 dissecting microscope. Most illustrations of the genitalia were made using an Olympus BH-2 compound microscope fitted with a camera lucida. Specimens were temporarily cleared in methyl salicylate (Holm 1979), then positioned for illustration on a temporary slide using the method described in Coddington (1983). The illustration of the epi-

gynum in ventral view was based on photographs taken using a Nikon DXM 1200F digital camera mounted on a Leica MZ 16. The photograph of the cleared epigynum was taken using the digital camera mounted on an Ortholux II compound microscope; multiple images were combined using Auto-Montage by Syncroscopy (version 4.01). SEM images were taken using the AMRAY 1800 at the National Museum of Natural History Scanning Electron Microscope Facility.

All measurements are in millimeters and were taken using a reticle mounted in a Leica MZ APO dissecting microscope. The position of the first metatarsal trichobothrium (TmI) is expressed as the ratio of the distance between the proximal margin of the metatarsus and the root of the trichobothrium divided by the total length of the metatarsus (Denis 1949; Locket & Millidge 1953).

**Material examined.**—When multiple consecutive records in the material examined section were from the same locality, the locality

data after the first record is given in brackets as [same locality]. When data labels did not include geographic coordinates, I attempted to determine the approximate location using maps, gazetteers, and other literature. Once the location was inferred, the coordinates were included in [square brackets]; coordinates taken directly from the data label are given in (parentheses). When no coordinates could be determined for any cave within a county, a dot near the geographic center of the county was included in the map (Fig. 1). In most cases, coordinates will not be precise enough that readers will be able to locate caves without additional information. The map was created using ArcView version 8.3.

**Phylogenetic analysis.**—*Porrhomma cavernicola* was coded into the phylogenetic data matrix of Miller (2005); no new characters were added to the analysis. The expanded analysis consists of 87 taxa coded for 176 characters, 172 of which are phylogenetically informative. The majority of characters concern the male genitalia, somatic morphology, and female genitalia; a few characters concern behavior and web architecture. See (Miller & Hormiga 2004) for descriptions of characters and character states. *Porrhomma cavernicola* was coded as follows: 0000001000 0401010–01 1001000010 0000000101 1000000001 1100100000 0–00000–0 0012001000 0–00000001 0100100100 000000000? 2100011 000 0041011111 3211111111 1111100000 000?000–00–201110011? ??????. Analysis was conducted using heuristic searches in PAUP\* (1000 replicates of random taxon addition; Swofford 2001). All characters were treated as unordered and equally weighted.

**Abbreviations.**—The following anatomical abbreviations are used in the text and figures: A = atrium; AC = aciniform gland spigot; AG = aggregate gland spigots; ALE = anterior lateral eye; AME = anterior median eye; ARP = anterior radical process; CD = copulatory duct; CL = column; DP = dorsal plate of epigynum; DSA = distal suprategular apophysis; E = embolus; EM = embolic membrane; F = fundus; FE = femur; FL = flagelliform gland spigot; FD = fertilization duct; MT = metatarsus; PA = patella; PC = paracymbium; PLE = posterior lateral eye; PME = posterior median eye; PT = protegulum; R = radix; S = spermatheca; SPT = suprategulum; ST = subtegulum; T = tegul-

um; TA = tarsus; TI = tibia; TLL = total leg length; TmI = position of first metatarsal trichobothrium; TmIV = fourth metatarsal trichobothrium; TP = tailpiece of radix; VP = ventral plate of epigynum. Institutional abbreviations are given in the Acknowledgments.

## TAXONOMY

### Family Linyphiidae Blackwall 1859

#### Genus *Porrhomma* Simon 1884

*Porrhomma* Simon 1884: 360. Type species *Linyphia proserpina* Simon 1873 (= *Erigone convexa* Westring 1851, synonymy in Holm 1944: 130, 133) by subsequent designation (Simon 1894: 701).

*Opistoxys* Simon, 1884: 373. Type species *Opistoxys acuta* Simon 1884 (= *Linyphia microphthalmia* O. Pickard-Cambridge 1871, synonymy in Thaler 1975: 142) by monotypy. Synonymy in Thaler 1975: 142.

**Remarks.**—The Holarctic genus *Porrhomma* consists of 31 species plus one subspecies (Platnick 2004). The species of the genus tend to be quite homogeneous, but within species, the genitalia tend to exhibit a high degree of variation. Species range in total length from about 1.2–3.2. Most species are epigean, found mostly in cool, mesic habitats including forests, grasslands, and under stones. Some species are troglomorphic [e.g., *P. convexum* (Westring 1861) and *P. egeria* Simon 1884], while others are troglobites [e.g., *P. cavernicola* and *P. rosenhaueri* (L. Koch 1872)].

#### *Porrhomma cavernicola* (Keyserling 1886)

Figs. 1–26

*Linyphia incerta* Emerton 1875:280, figs. 13–21 (♂, ♀); Packard 1875:275; Packard 1888:57; MacCook 1890:292, figs. 284–285; Simon 1894:690. *Willibaldia incerta* (Emerton): Keyserling 1886: 123; Marx 1890:531; Banks 1910:32.

*Willibaldia cavernicola* Keyserling 1886:123–124, pl. 15, fig. 204 (♀); Packard 1888:58; Marx 1890: 531; Comstock 1903:32; Banks 1907:739, Banks 1910:32; Comstock 1913:383; Comstock 1948: 397; Bonnet 1959:4721.

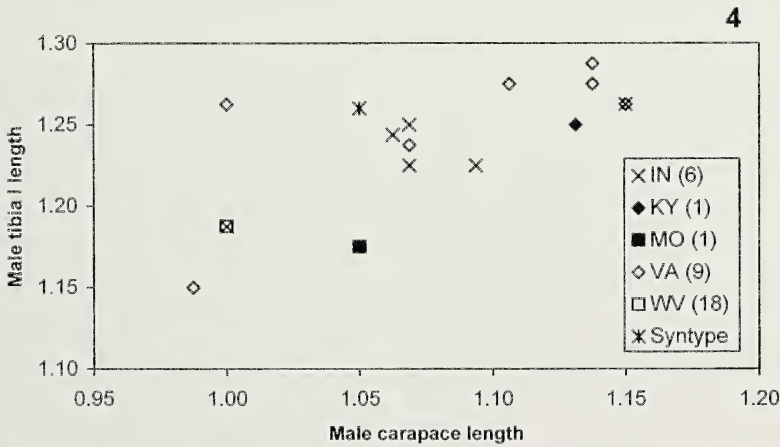
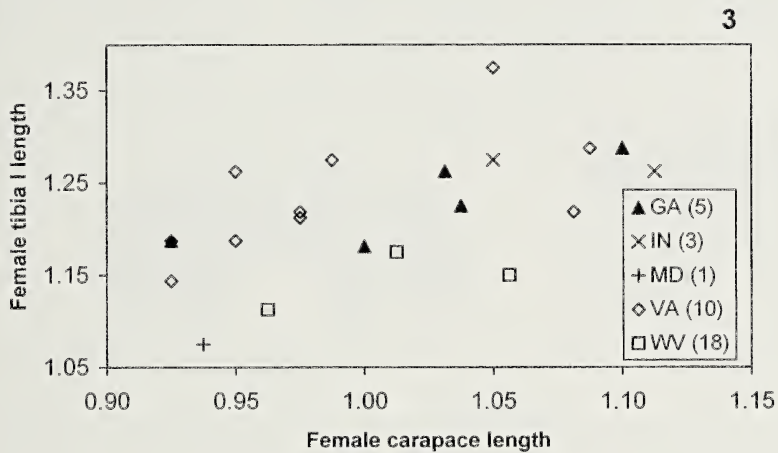
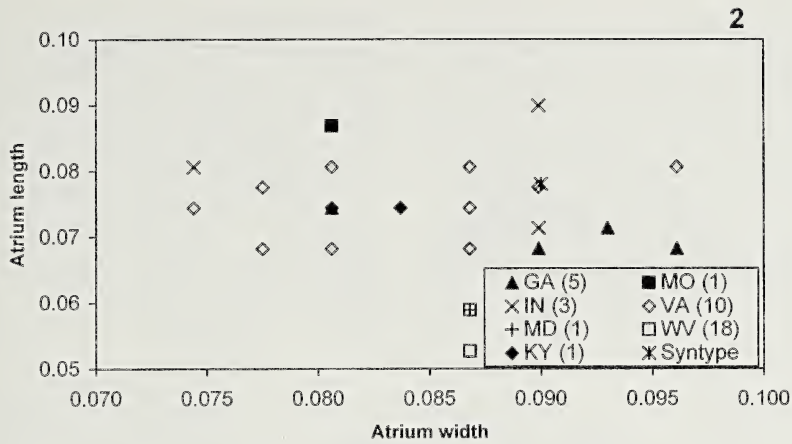
*Taranuncus cavernicola* (Keyserling): Simon 1894: 690.

*Troglohyphantes cavernicola* (Keyserling): Simon 1894:706; Crosby 1905:368, figs. 20–22 (♂); McIndoo 1910:304; McIndoo 1911a:183; McIndoo 1911b:391.

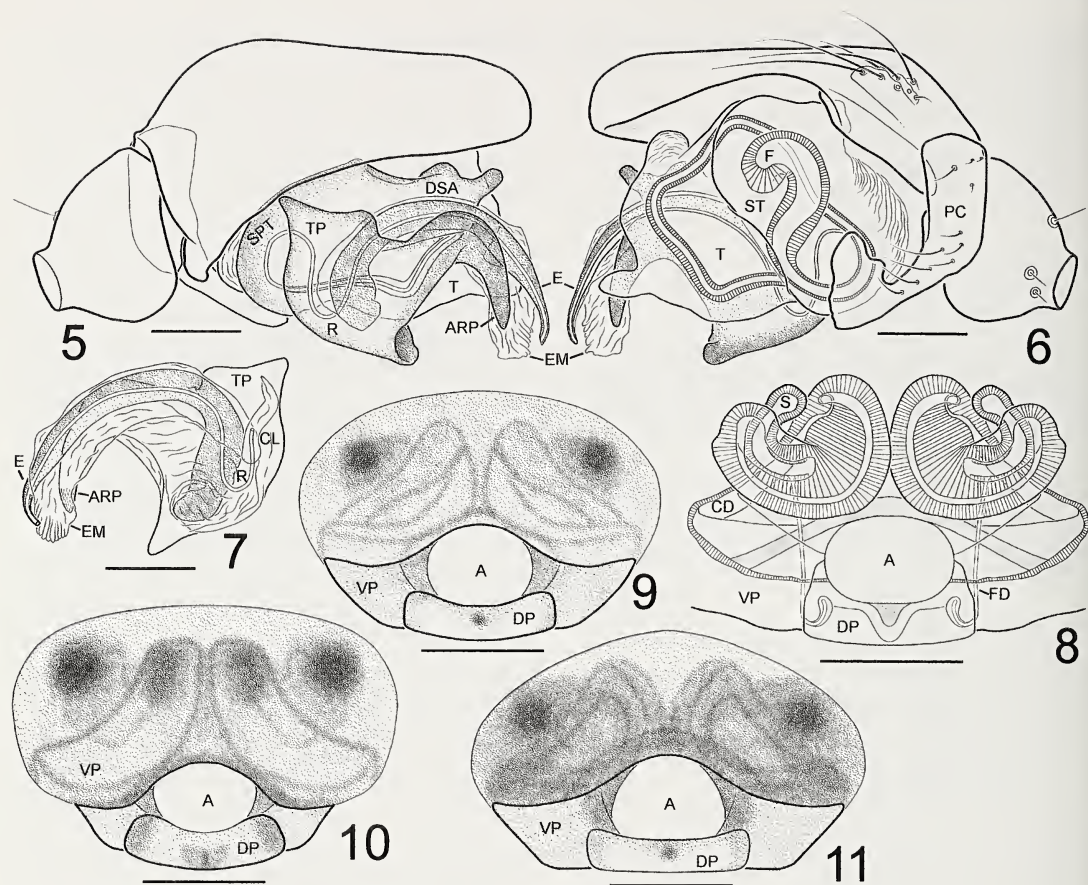
*Troglohyphantes incertus* (Emerton): Comstock 1903:32; Comstock 1913:383; Petrunkevitch 1911:272.

*Troglohyphantes cavernicolus* (Keyserling): Com-





Figures 2-4.—Morphometric variation of selected features in *Porrhomma cavernicola*. Individuals grouped by state with sample size in parentheses. The syntype specimens of *Willibaldia cavernicola* are indicated by an asterisk symbol. 2. length and width of the atrium, female epigynum; 3. tibia I length and carapace length in female; 4. tibia I length and carapace length in male.



Figures 5–11.—*Porrhomma cavernicola* (Keyserling). 5–7. left male palp; 8–11. epigynum. 5. prolateral view; 6. retrolateral view; 7. embolic division, mesal view; 8. dorsal view; 9–11. ventral view. 5–9. from Sam Six Cave, Wythe County, Virginia; 10. from McFerrin Breakdown Cave, Greenbrier County, West Virginia; 11. from El Rod Cave, Orange County, Indiana. Scale bars = 0.1 mm. See text for abbreviations.

stock 1903:32; Comstock 1913:383; Petrunkevitch 1911:272; Elliott 1932:425.

*Willibaldi cavernicola* (Keyserling): Banta 1907:62.

*Porrhomma incerta* (Emerton): Berland 1931:384.

*Porrhomma cavernicola* (Keyserling): Roewer 1942:603; Platnick 2004.

*Porrhomma emertoni* Roewer 1942:603 (replacement name for *Linyphia incerta* Emerton 1875, preoccupied by *Linyphia incerta* Walckenaer 1842, nomen dubium, see van Helsdingen 1972); Platnick 2004. **NEW SYNONYMY.**

*Porrhomma incertum* (Emerton): Bonnet 1958: 3756.

**Justification of Synonymy.**—Berland (1931) noted that the two nominal taxa appear to differ very little, but he did not synonymize them. After examination of the types and other specimens, I found no morphological evidence to maintain two diagnosable species of

troglobitic *Porrhomma* in the Appalachian region. Selected morphometric characteristics failed to show any regional pattern that might indicate multiple species (Figs. 2–4). A similar approach did reveal the presence of multiple species in troglobitic *Anthrobia* (Miller 2005).

**Nomenclature.**—*Linyphia incerta* Emerton 1875 is a primary homonym of *Linyphia incerta* Walckenaer 1842 and is therefore permanently invalid (International Commission on Zoological Nomenclature 1999, Article 57.2). Roewer (1942) proposed *Porrhomma emertoni* Roewer 1942 as a replacement name for *L. incerta*. *Willibaldia cavernicola* Keyserling 1886 has priority over *P. emertoni*.

**Types.**—UNITED STATES: *Kentucky*: Barren County, Reynolds Cave (BMNH,



1890.7.1.8242–8243, syntypes of *Willibaldia cavernicola*, examined), 1 ♂, 1 ♀. General condition degraded; male abdomen missing, as are most legs for both specimens; female prosoma and abdomen disarticulated. *Male*: Carapace 1.05 long, 0.76 wide, tibia I 1.26. *Female*: Carapace 1.16 long, 0.78 wide, atrium 0.078 long, 0.090 wide.

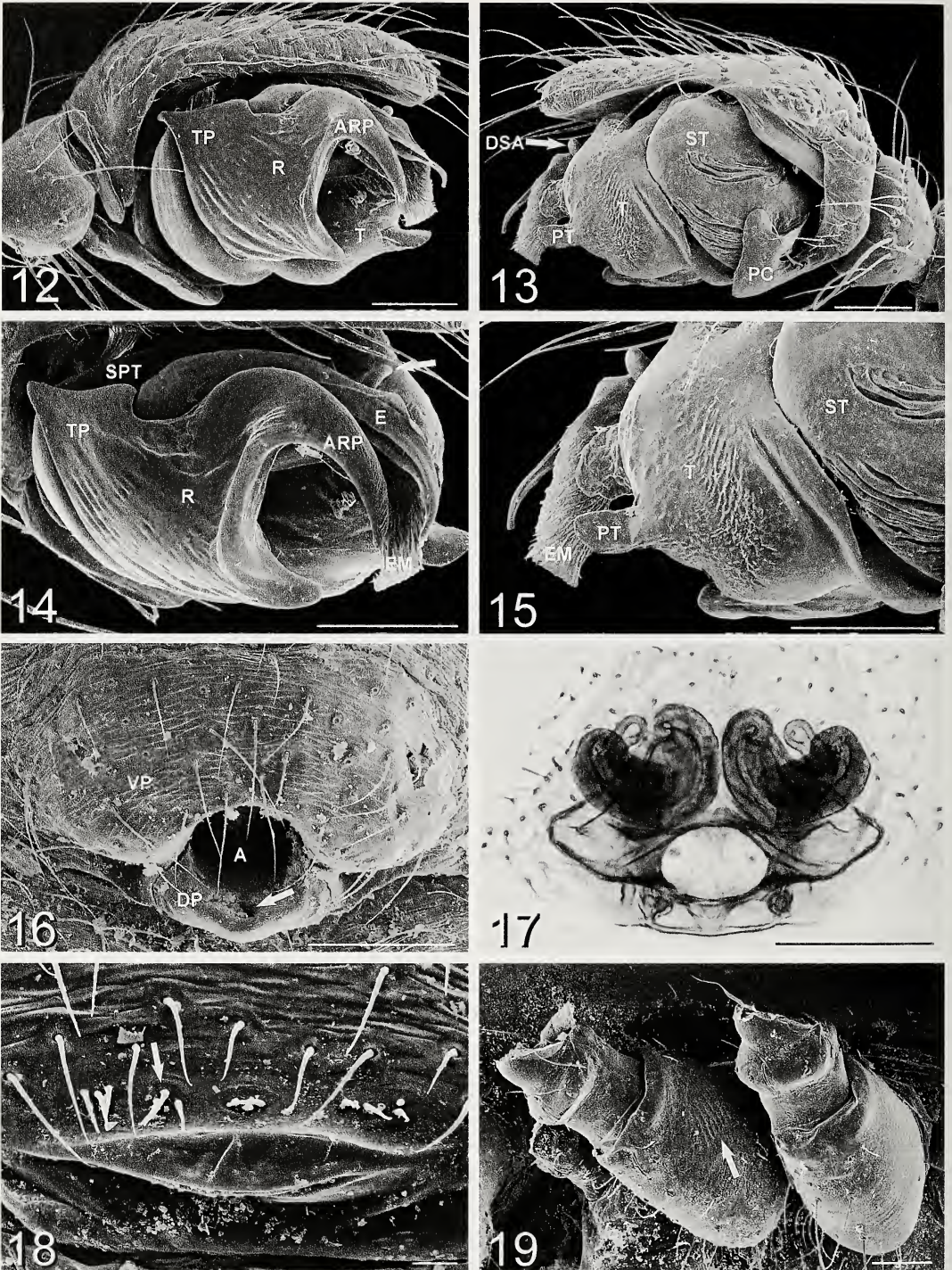
*Virginia*: Augusta County, Fountain Cave [38°10'N, 78°55'W], Packard (MCZ, syntypes of *Linyphia incerta*, examined), 2 ♂, 4 ♀, 5 juveniles.

**Additional Material Examined.**—UNITED STATES: *Georgia*: Bartow County, Kingston Saltpeter Cave (34°12'N, 84°54'W), 2 June 1999, W. Reeves (USNM), 5 ♀. *Indiana*: Lawrence County, JJ's Sister Cave (38°45'N, 86°36'W), 26 August 2004, J. Miller (USNM), 1 ♂; Orange County, El Rod Cave (38°37'N, 86°31'W), 26 August 2004, P. Paquin, J. Miller, J. Lewis, N. Dupérré (USNM), 4 ♂, 1 ♀, 3 juveniles; [same locality], inside cave, shallow cave, hand collecting, P. Paquin, N. Dupérré (USNM, PP-2304), 2 ♀, juveniles. *Kentucky*: Carter County, Carter Cave, A Cave [38°22'N 83°07'W], Packard (MCZ), 1 ♂, 2 ♀. *Maryland*: Garrett County, Crabtree Cave, 24 September 1987, pool surface, right passage, D. Feller (USNM, 51B), 1 ♀; Washington County, Fairview Cave, 30 September 1988, pool surface, mudslide area, D. Feller (USNM, 131C), 1 ♀. *Missouri*: Boone County, Rocheport Cave, 3 miles below Rocheport [38°55'N, 92°30'W], 23 July 1905, C.R. Crosby (MCZ), 1 ♂, 1 ♀. *Virginia*: Augusta County, Fountain Cave [38°10'N, 78°55'W], (MCZ), 1 ♂; Page County, Lurray [sic, Luray] Cave [38°39'N, 78°29'W], Kochele (USNM, 187), 2 ♀ [in two vials]; Page County, Luray Cave [38°39'N, 78°29'W], R.V. Chamberlin (MCZ, 59645), 1 ♂, 2 ♀; Montgomery County, Aunt Nelli's hole (37°12'N, 80°22'W), 5 September 2004, P. Paquin, J. Miller, N. Dupérré, R. Storey (USNM), 1 ♂, 1 juvenile; [same locality], 5 September 2004, inside cave, hand collecting, P. Paquin, N. Dupérré (USNM, PP-4304), 1 ♀; Russell County, Cartop Cave, 26 November 1999, D. Hubbard (USNM), 3 ♂, 2 ♀, 3 juveniles; Russell County, Maggie Baker Cave, 17 September 1997, D. Hubbard (USNM), 3 ♀; Scott County, Abram's Cave, 15 December 1999, D. Hubbard (USNM), 1 ♂; Scott County, Little Duck Cave, 28 November 1997, D. Hubbard

(USNM), 2 ♂, 1 ♀; Scott County, Queens Cave, 15 April 1997, D. Hubbard (USNM), 1 ♀; Washington County, Robinson Cave, 25 February 1997, D. Hubbard (USNM), 1 ♂; Wythe County, Sam Six Cave, 25 November 1998, D. Hubbard (USNM), 1 ♂, 2 ♀, 3 juveniles. *West Virginia*: Greenbrier County, McFerrin Breakdown Cave, 22 August 2004, visual, E. Saugstad, K. Schneider (USNM), 1 ♀; Mineral County, High Rock Fissure Cave, 30 October 1988, woodrat midden, rope drop, D. Feller (USNM, 133B), 1 ♂; Monroe County, Steeles Cave, 11 June 2004, visual (USNM), 1 ♂, 2 ♀. Two additional vials had no locality data: 1 ♂, 1 ♀, Banks (MCZ, 57184, 1753); 1 ♀, Banks (MCZ, 59646).

**Additional Records.**—The following records were compiled from literature sources (McIndoo 1910; Holsinger et al. 1976; Holsinger & Culver 1988). UNITED STATES: *Indiana*: Lawrence County, Shawnee Cave [now called Donaldson Cave], 3 miles E Mitchell. *Tennessee*: Claiborne County: Jennings Cave [36°33'N, 83°30'W]; Hawkins County: Sensabaugh Saltpeter Cave [36°34'N, 82°39'W]. *Virginia*: Augusta County: Glade Cave, Madisons Saltpeter Cave; Bath County: Clark's Cave [38°5'N, 79°39'W], Crossroads Cave, Porters Cave, Witheros Cave, Baner Spring Cave, Coon Cave; Craig County: New Castle Murder Hole Cave, Rufe Caldwell Cave; Frederick County: Beans Cave [39°9'N, 78°21'W]; Giles County: Clover Hollow Cave [37°19'N, 80°28'W]; Lee County: Unthands Cave, Fisher Cave; Page County: Luray Caverns [38°39'N, 78°29'W]; Ruffners Cave No. 1; Roanoke County: Dixie Caverns [37°9'N, 80°9'W]; Rockbridge County: Bell Cave [37°45'N, 79°22'W], Buck Hill Cave [37°36'N, 79°34'W]; Rockingham County: Three-D Maze Cave [38°30'N, 78°45'W]; Tazewell County: Gully Cave [37°2'N, 81°38'W], Lawson Cave [37°5'N, 81°21'W]; Wise County: Parsons Cave [36°51'N, 82°42'W]. *West Virginia*: Berkeley County: Whittings Neck Cave [39°30'N, 77°50'W]; Grant County: Klines Gap Cave [39°4'N, 79°14'W]; Greenbrier County: Bransfords Cave [38°0'N, 80°30'W], Higginbothams Cave [37°56'N, 80°24'W], Organ Cave [37°43'N, 80°26'W], Pollock Cave [37°45'N, 80°37'W], Pollock Saltpeter Cave; Monroe County: Fulton Cave [37°32'N, 80°27'W]; Pendleton County: Moyers Cave [38°34'N,





Figures 12-19.—*Porrhomma cavernicola* (Keyserling); 12-16, 18, 19. scanning electron micrographs; 12. photograph. 12-15. left male palp; 16, 17. epigynum; 18. epiandrous region of male; 19. coxa, trochanter I and II of female. 12. prolateral view; 13. retrolateral view; 14. embolic division, arrow indicates DSA; 15. detail of tegulum; 16. ventral view, arrow indicates socket in dorsal plate; 17. dorsal view, cleared; 18. arrow indicates epiandrous gland spigots; 19. arrows indicate striae on coxa I. 12-15. from High Rock Fissure Cave, Mineral County, West Virginia; 16, 19. from Fairview Cave, Washington County, Maryland; 17. from Cartop Cave, Russell County, Virginia; 18. from Sam Six Cave, Wythe County, Virginia. Scale bars = 0.01 mm (Fig. 18); 0.1 mm (Figs. 12-17, 19). See text for abbreviations.



79°22'W], Mystic Cave [38°49'N, 79°26'W], Schoolhouse Cave [38°47'N, 79°47'W], Seneca Caverns [38°47'N, 79°21'W], Stratosphere Balloon Cave [38°46'N, 79°20'W]; Pocahontas County: Sharps Cave [38°25'N, 80°5'W].

**Diagnosis.**—Troglobite distinguished from other *Porrhomma* species in North America by the extreme reduction of the eyes (Figs. 20–22). Note that *P. rosenhaueri* L. Koch 1872, a cave associated species from Europe and Russia, also has reduced eyes (Locket & Millidge 1953, Wiehle, 1956, Roberts 1993, Platnick 2004). Males of *P. cavernicola* have the ARP much thicker and more ventrally-directed compared to *P. rosenhaueri* (see Roberts 1993, fig. 59E).

**Description.**—*Male (from Sam Six Cave, Wythe County, Virginia):* Total length 2.43. Carapace 1.19 long, 0.85 wide, orange, squamate to reticulate texture. Abdomen white. Eyes minute, laterals separated (see variation, below). Hairs on clypeus and ocular region relatively long (Fig. 20). Sternum 0.58 long, 0.58 wide, light orange. Coxa I with stridulatory striae on posterior face (as in Fig. 19). Coxa IV separation 0.93 times their width. Chelicerae orange, with three promarginal teeth, four retromarginal teeth; stridulatory striae scale-like (as in Figs. 24, 25). Sulcus present on margin of carapace posterior to chelicerae (as in Fig. 23). Legs orange, tibia I 12.25 times longer than thick; TmI 0.43. Leg I: FE 1.31, PA 0.29, TI 1.23, MT 1.10, TA 0.70, TLL 4.63; leg II: FE 1.23, PA 0.29, TI 1.13, MT 1.10, TA 0.68, TLL 4.63; leg III: FE 1.11, PA 0.25, TI 0.90, MT 0.86, TA 0.56, TLL 3.69; leg IV: FE 1.30, PA 0.28, TI 1.29, MT 1.13, TA 0.68, TLL 4.66. Epiandrous gland spigots present (Fig. 18). Anterior lateral spinnerets with five aciniform, flagelliform, and two aggregate gland spigots (Fig. 26); posterior median spinnerets with minor ampullate, two aciniform gland spigots. Palpal tibia with one prolateral, two retrolateral trichobothria (Fig. 6); tibial apophysis absent. Retrobasal region of cymbium with short apophysis bearing long setae and glabrous region along margin (Fig. 13). Paracymbium hook-like, proximal part clothed with macrosetae (Fig. 13). Subtegulum ectal to tegulum. Retrolateral part of tegulum partially covered in fine ridges (Fig. 15). Protegulum plus one other distal apophysis of the tegulum present (Fig. 15). Suprattegulum continuous with te-

gulum, distal suprattegular apophysis finger-like, projecting distally (Figs. 5, 14). Embolic division a plate-like radix with a short, posterior-projecting tailpiece and a long curved anterior radical process (Fig. 12). Basal part of embolus broadly articulated to radix by a membrane (Fig. 7); distal part of embolus partially wrapped by embolic membrane, which is covered in fine papillae (Fig. 14).

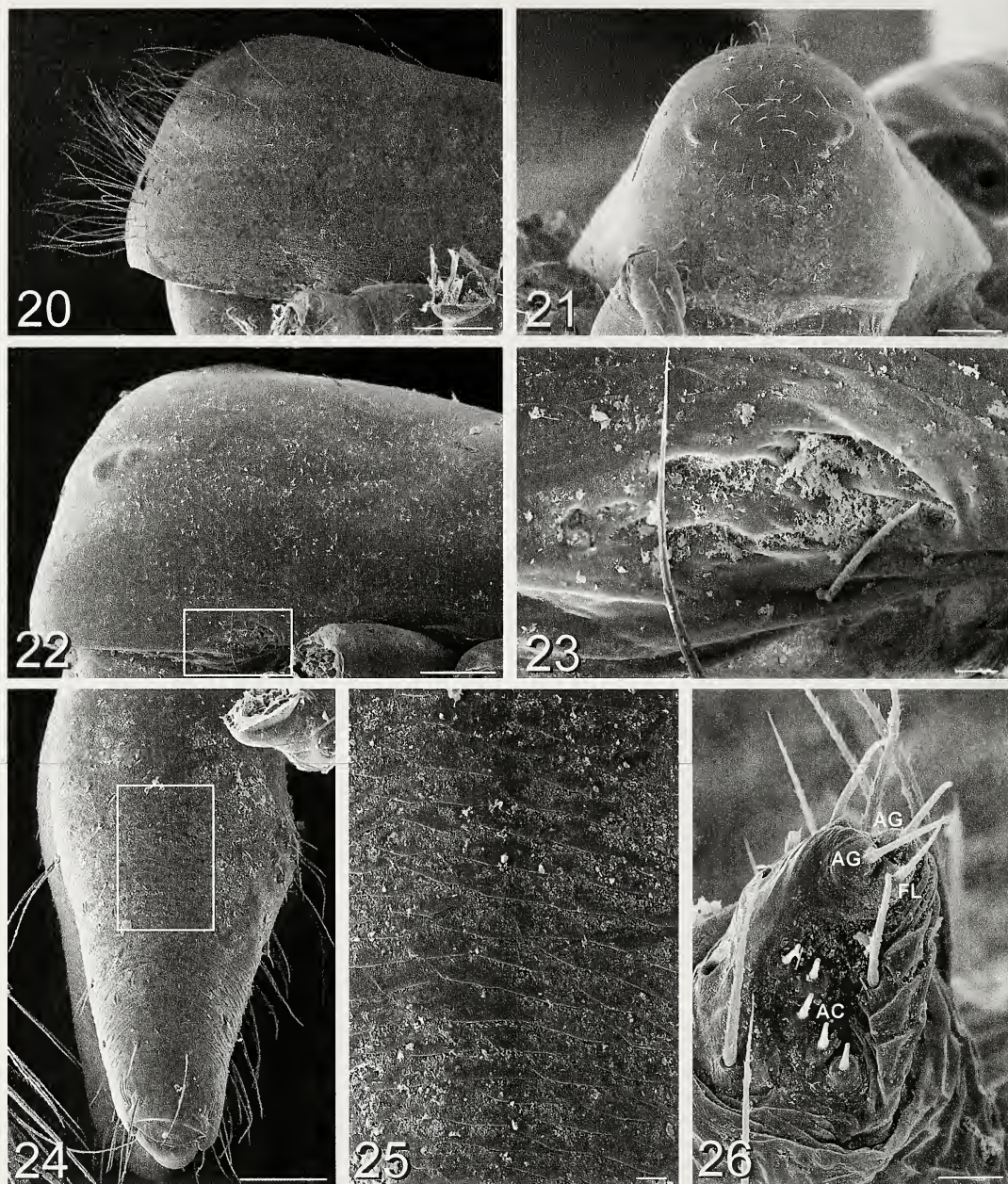
*Female (same locality as male):* Total length 2.55. Carapace 1.13 long, 0.79 wide, orange, squamate to reticulate texture. Abdomen white. Eyes minute, laterals separated (see variation, below). Hairs on clypeus and ocular region not as long as in male (Figs. 21, 22). Sternum 0.54 long, 0.55 wide, orange. Coxa I with stridulatory striae on posterior face (Fig. 19). Coxa IV separation 1.00 times their width. Chelicerae orange, with three promarginal teeth, four retromarginal teeth; stridulatory striae scale-like (Figs. 24, 25). Sulcus present on margin of carapace posterior to chelicerae (Figs. 22, 23). Legs orange, tibia I 12.13 times longer than thick; TmI 0.44. Palpal tibia with one prolateral, two retrolateral trichobothria; palpal tarsus with two dorso-mesal, two dorsoectal macrosetae, four ventro-mesal, two ventroectal macrosetae, claw absent. Leg I: FE 1.29, PA 0.29, TI 1.21, MT 1.05, TA 0.46, TLL 4.51; leg II: FE 1.26, PA 0.29, TI 1.13, MT 0.99, TA 0.64, TLL 4.30; leg III: FE 1.09, PA 0.28, TI 0.86, MT 0.81, TA 0.54, TLL 3.58; leg IV: FE 1.31, PA 0.26, TI 1.28, MT 1.10, TA 0.66, TLL 4.61. Epigynum with deep circular atrium (Figs. 9–11, 16). Dorsal plate with socket (Fig. 16). Spermathecae crescent-shaped (Figs. 8, 17). Fertilization ducts arise from posterior part of spermathecae, long, straight, recurved terminally (Fig. 8). Copulatory ducts follow complex path, heavily sclerotized proximally, wider and less sclerotized close to atrium (Fig. 8).

*Chaetotaxy:* Femur I with one or two dorsal, two prolateral macrosetae; femur II with one or two dorsal macroseta. Tibia I and II with two dorsal, one prolateral, one retrolateral macrosetae; tibia III and IV with two dorsal macrosetae. TmIV absent.

*Tracheae:* Haplotracheate, four unbranched trunks confined to abdomen.

**Variation.**—Some or all eyes may be absent; eye loss not always bilaterally symmetrical. Variation in epigynum illustrated in Figs 2, 9–11.





Figures 20–26.—*Porrhomma cavernicola* (Keyserling); scanning electron micrographs. 20. male prosoma; 21–23. female prosoma, box in 22 defines area of image 23; 24, 25. female chelicera, box in 23 defines area of image 25; 26. anterior lateral spinneret of male. 20, 22. lateral view; 21. anterior view; 23. sulcus; 24. lateral; 25. detail. 20, 26 from Cartop Cave, Russell County, Virginia; 21, 24, 25. from Queens Cave, Scott County, Virginia; 22, 23. from Fairview Cave, Washington County, Maryland. Scale bars = 0.01 mm (Figs. 23, 25, 26); 0.1 mm (Figs. 20–22, 24). See text for abbreviations.

**Natural History.**—McIndoo (1910) reported that *P. cavernicola* “. . . are found only in total darkness, where the atmosphere is saturated. . .” McIndoo described the web as a

sheet, slightly curved downward with the spider on the underside.

**Distribution.**—Known from caves in Georgia, Indiana, Kentucky, Maryland, Missouri,



Tennessee, Virginia, and West Virginia (Fig. 1).

DISCUSSION

**Phylogenetic Relationships and Character Evolution.**—Analysis of the expanded data matrix (Miller 2005 plus *P. cavernicola*; see also Miller & Hormiga 2004) yielded a single most parsimonious tree (L = 931, CI = 0.23, RI = 0.59; with four autapomorphic characters excluded: L = 927, CI = 0.23; Fig. 27). The topology is identical to that found in Miller (2005) with *Porrhomma* placed sister to a clade consisting of Mynogleninae plus Erigoninae. *Porrhomma* has traditionally been placed in the Linyphiinae (e.g., Merrett 1963; Millidge 1977; Brignoli 1983). *Porrhomma* does not form a monophyletic group with the linyphiines included in the analysis (Fig. 27). Admittedly, this analysis suffers from sparse taxon sampling among non-erigonine linyphiids so the conclusions presented here must be considered preliminary. More robust taxon sampling from a variety of non-erigonine linyphiids plus the addition of molecular sequence data is called for.

Miller & Hormiga (2004) added taxa and characters to a previous analysis of erigonine relationships (Hormiga 2000). Considering only taxa common to both studies, relationships changed dramatically from one study to the next. Miller & Hormiga (2004) investigated whether the addition of taxa, characters, or both were primarily responsible for the changes in the tree. They concluded that most of the changes were due to the addition and modification of characters, not the addition of taxa. Miller (2005) added four taxa from the genus *Anthrobia* to the Miller & Hormiga (2004) matrix. Consistent with the conclusions of Miller & Hormiga (2004) about the relative insensitivity of their topological results to the addition of taxa, relationships of taxa included in both analyses were identical. For this study, one additional taxon has been added. Again, relationships among previously-included taxa are unchanged.

Hormiga (1999) reported the presence of lateral sulci at the margin of the prosoma in both males and females in *Porrhomma* (Figs. 22, 23), as well as *Bathypantes* Menge 1866, *Diplostyla* Emerton 1882, *Kaestneria* Wiehle 1956, *Pacifiphantes* Eskov & Marusik 1994, and *Vesicapalpus* Millidge 1991. Hormiga

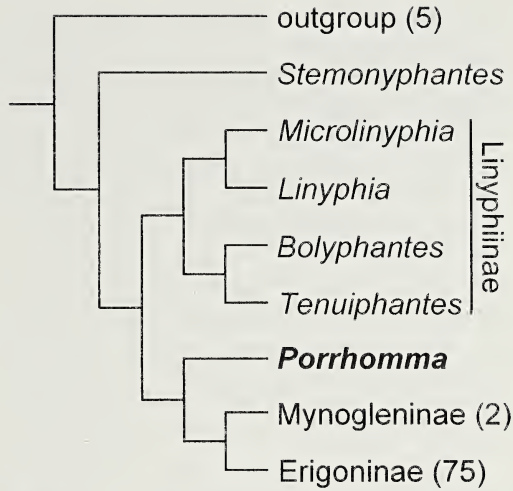


Figure 27.—Summary of phylogenetic analysis results showing the position of *Porrhomma*. Labels representing multiple terminals have the number of taxa in parentheses. See Miller (2005) for a more detailed tree figure (without *Porrhomma*); see Miller & Hormiga (2004) for characters and states.

(1999) pointed out that these sulci represent a derived trait, potentially supporting the monophyly of genera exhibiting these sulci.

Males of *Porrhomma cavernicola* retain the triplet, one flagelliform and two aggregate gland spigots necessary for making araneoid sticky silk (Fig. 26; Coddington 1989). The triplet is not found in males of true linyphiines, but is retained in the enigmatic genus *Stemonyphantes* Menge 1866, most erigonines, and in the two mynoglenine genera that have been investigated (Hormiga 2000). It would be useful to investigate the male spinnerets in *Bathypantes* and other genera known to have lateral sulci.

Males of *P. cavernicola* have epiandrous gland spigots (Fig. 18); the loss of these spigots is considered a synapomorphy of Erigoninae (Miller & Hormiga 2004).

*Porrhomma cavernicola* lack a tarsal claw on the female pedipalp. Previous phylogenetic analyses concluded that the loss of the tarsal claw was a synapomorphy for Erigoninae (e.g., Hormiga 2000; Miller & Hormiga 2004). The distribution of the tarsal claw on the tree (Fig. 27) makes this conclusion ambiguous. Either the claw was lost independently in the branches leading to erigonines and *Porrhomma*, or the claw was regained in mynoglenines.

**An Unusual Stridulatory Organ.**—Bishop (1925) described the trochanter II-coxa I stridulatory organ (Fig. 19). Although he attributed the organ to members of the genus *Troglohyphantes*, not *Porrhomma*, Bishop was almost certainly observing *P. cavernicola*. In 1925, *P. cavernicola* (under two names) was placed in *Troglohyphantes*; no other *Porrhomma* species was placed in *Troglohyphantes* at that time (Platnick 2004). Legendre (1963) reviewed sound production in spiders, including the trochanter II-coxa I organ. Citing Bishop (1925), Legendre attributed this organ to *Troglohyphantes* in Europe. However, this organ has not been described for *Troglohyphantes* in its current circumscription (Deeleman-Reinhold 1978, Platnick 2004) or for any other linyphiid genus I am aware of. The organ can be found in at least some epigeal *Porrhomma* species (Scharff, pers. comm.). No epigeal *Porrhomma* has ever been classified as in *Troglohyphantes*.

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**THE FOSSIL SPIDER FAMILY LAGONOMEGOPIDAE  
IN CRETACEOUS AMBERS WITH DESCRIPTIONS  
OF A NEW GENUS AND SPECIES FROM MYANMAR**

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**ABSTRACT.** The spider family Lagonomegopidae was described a decade ago from two specimens in Upper Cretaceous Siberian amber from the Taimyr Peninsula, and placed in the superfamily Palpimanoidea. Lagonomegopidae is known only from Cretaceous amber. Undiscovered extant species are considered unlikely because of their frequent occurrence in Cretaceous ambers and their absence in Tertiary fossil resins. One aim of this paper is to bring the existence of this family to the attention of neo-arachnologists. *Burlagonomegops eskovi* new genus and species is described from Cretaceous amber of Myanmar (Burma) and *Lagonomegops americanus* new species is assigned to a previously described, but unnamed specimen from Cretaceous New Jersey amber.

**Keywords:** Burma, Mesozoic, paleontology, Palpimanoidea

It is seldom the case that systematists working on extant spiders acknowledge the existence of fossil spiders in published papers on their particular group of interest. However, this is not universal and I am encouraged by the increased frequency with which reference to fossils now occurs. The 21<sup>st</sup> European Colloquium of Arachnology, Russia 2003, hosted the first special symposium dedicated to paleoarachnology (see Logunov & Penney 2004), which was well attended. It is often true that fossil spiders preserved in shales and other sediments can be difficult, if not impossible to place in the framework of higher level extant spider taxonomy and systematics. However, this is not always the case with amber-preserved spiders. Marusik & Penney (2004) noted that fossil and Recent arachnological taxonomy cannot be considered as totally independent disciplines. The importance of considering fossils became evident when the fossil genus *Archaea* Koch & Berendt 1854, first described from Baltic amber (and placed in Archaeidae, a new family erected for the fossils) was shown to be a senior synonym of the extant genus *Eriauchenius* O. Pickard-Cambridge 1881 (originally placed in Theridiidae) described from Madagascar by Simon (1895). More recently, the new name *Theridion sulawesiense* Marusik & Penney 2004 was erected for the extant spider species *T.*

*simplex* Thorell 1877 from Sulawesi because that name was preoccupied by *T. simplex* Koch & Berendt 1854 from Baltic amber.

Fossil spiders in Cenozoic ambers have been known for centuries. The first major work with formal descriptions appeared in the mid nineteenth century (Koch & Berendt 1854). In contrast, it was only a decade ago that the first spider inclusion in Mesozoic amber was described, by Eskov & Wunderlich (1995) of Santonian age from Siberia. However, it is only within the last few years that new descriptions of Cretaceous amber spiders have been published, for example in fossil resins of Turonian age from New Jersey (Penney 2002, 2004a), Barremian age from the Isle of Wight (Selden 2002), Upper Neocomian–basal Lower Aptian age from Lebanon (Penney & Selden 2002; Penney 2003a; Wunderlich & Milki 2004 [not 2001 as cited by Poinar & Milki 2001]), Albian age from Myanmar (Penney 2003b, 2004b) and Campanian age from Canada (Penney 2004c). Spiders have been listed as present (and occasionally figured) in Mesozoic amber faunas from Canada (McAlpine & Martin 1969), the Caucasus (Eskov & Wunderlich 1995), France (Schlüter 1978; Néraudeau et al. 2002; Perrichot 2004), Álava, Spain (Alonso et al. 2000) and Asturias, Spain (Arbizu et al. 1999) but none of these have yet been formally described.

The enigmatic spider family Lagonomegopidae was first described by Eskov & Wunderlich (1995) from two specimens in Upper Cretaceous Siberian amber from the Taimyr Peninsula, and placed in the superfamily Palpimanoidea based on the presence of peg teeth, the absence of teeth on the cheliceral promargin, the trichobothrial pattern and the spineless legs. Penney (2002) described an additional specimen from New Jersey amber as *Lagonomegops* sp. indet. and Penney (2004c) described *Grandoculus chemahawinensis* Penney 2004 from Canadian amber. Wunderlich (2004) provided the same figures and descriptions of the specimens originally described by Eskov & Wunderlich (1995). Platnick's (2004) catalog did not include fossil taxa and the publications in which this fossil family is described may not be immediately obvious (or available) to some arachnologists, because one is a private journal published in Germany, two are paleontological and the fourth is a privately published book. The main aim of this paper is to bring to the attention of the arachnological community the existence of the enigmatic spider family Lagonomegopidae, which is currently only known from amber, but which may have undiscovered extant species in the southern hemisphere, as in the Archaeidae mentioned above. In addition, new specimens are described for the first time from Cretaceous amber of Myanmar (Burma).

## METHODS

**Material.**—Two specimens preserved in Burmese amber (burmite) (for details of locality and stratigraphy, see Zherikhin & Ross [2000], Grimaldi et al. [2002], Cruickshank & Ko [2003]) held in the Department of Entomology at the American Museum of Natural History (AMNH). AMNH Bu-707 is preserved in a small piece (4 × 3 × 3 mm) of clear yellow-orange amber with no syninclusions, but with numerous small air bubbles; AMNH Bu-1353 is preserved in a small piece (9 × 5 × 5 mm) of clear yellow-orange amber containing several fracture planes and a male Diptera (Microphorinae) syninclusion.

**Methods.**—Prior to being received by the author the amber had been set in a clear plastic resin and cut and polished to reveal the inclusions. All measurements were made using an ocular graticule and are in mm. Drawings were done under incident light with a

*camera lucida* attached to an Olympus SZH stereomicroscope and photographs were taken with a Nikon D1X digital camera attached to a Wild M8 stereomicroscope.

**Abbreviations used in the figures.**—a = air bubble, ab = abdomen, car = carapace, L/R 1–4 = left and right walking legs 1–4, p = pedipalp, s = spine, t = trichobothrium.

## SYSTEMATIC PALEONTOLOGY

**Remarks.**—It is appreciated that fossil spiders are taxonomically subequal to the extant fauna (Eskov 1990) and the certainty with which pattern-based species can be recognized in the fossil record is less than that for extant organisms (Smith 1994). When I described the second known occurrence of the family Lagonomegopidae, from New Jersey amber (Penney 2002), I was reluctant to diagnose it as a species and refrained from naming it. However, given the recent discovery that this family represents a regular component of Cretaceous faunas from several geographically distinct amber deposits, I feel it is now justifiable to place the specimens within a provisional taxonomic framework. Unfortunately all specimens identified to date are immature. The genitalia are unknown for this family so the taxonomy is based on somatic characters.

### Superfamily Palpimanoidea

**Remarks.**—See Penney (2004c) for a discussion of the systematic placement of Lagonomegopidae in this superfamily.

### Family Lagonomegopidae Eskov & Wunderlich 1995

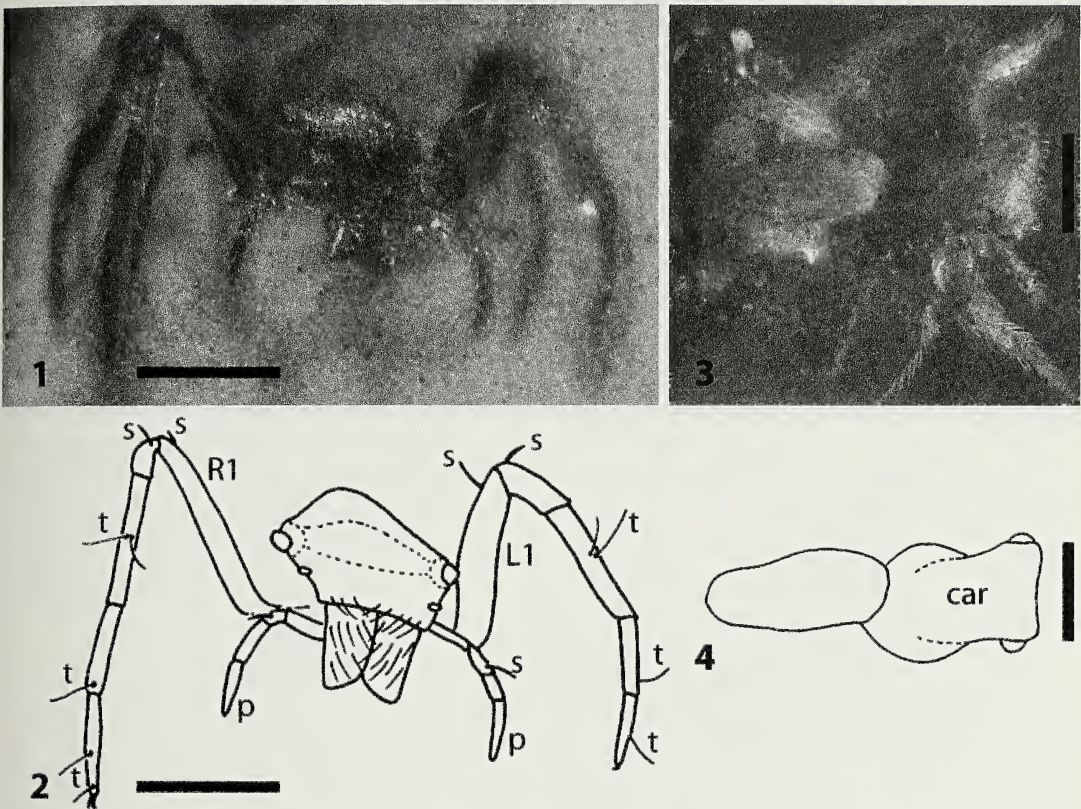
**Distribution.**—Fossil species in Cretaceous ambers from Siberia, New Jersey, Myanmar and Canada. Recent species not known.

### *Lagonomegops* Eskov & Wunderlich 1995

**Type species.**—*Lagonomegops sukatchevae* by original designation and monotypy. Holotype, juvenile, PIM 3311/564, held in the Paleontological Institute of the Russian Academy of Science, Moscow. Not examined because the current location of these specimens within the PIM collections is unknown (K. Eskov pers. comm. 2004).

**Distribution.**—Fossil species in Cretaceous ambers from Siberia and New Jersey. Recent species unknown.





Figures 1–4.—*Burlagonomegops eskovi* new species. Holotype, AMNH Bu-707, juvenile, Burmese amber. 1, 2. anterior view. 3, 4. dorsal view. 3–4. Scale lines = 0.5 mm

*Lagonomegops americanus* new species  
*Lagonomegops* sp. indet.: Penney 2002: 711, pl. 1 fig. 2, text-fig. 2.

**Material examined.**—Holotype juvenile, U.S.A.: New Jersey amber, 1995, K. Luzzi (AMNH NJ-556 (KL-297)).

**Diagnosis.**—*Lagonomegops americanus* can be distinguished from *L. sukatchevae* by the possession of the following combination of characters: tarsi longer than metatarsi, a single dorsal spine distally on femur 1.

**Etymology.**—The specific epithet is after America, the provenance of the fossil.

**Distribution and age.**—New Jersey amber; Turonian, Upper Cretaceous (Grimaldi et al. 2000).

*Burlagonomegops* new genus

**Type species.**—*Burlagonomegops eskovi* new species.

**Etymology.**—*Bur* derived from Burma, the

former name of Myanmar, and *lagonomegops*, the type genus of the family.

**Diagnosis.**—*Burlagonomegops* differs from the other genera in this family by having the carapace distinctly longer than wide and in possessing tarsal trichobothria.

**Description.**—See description of the type species below.

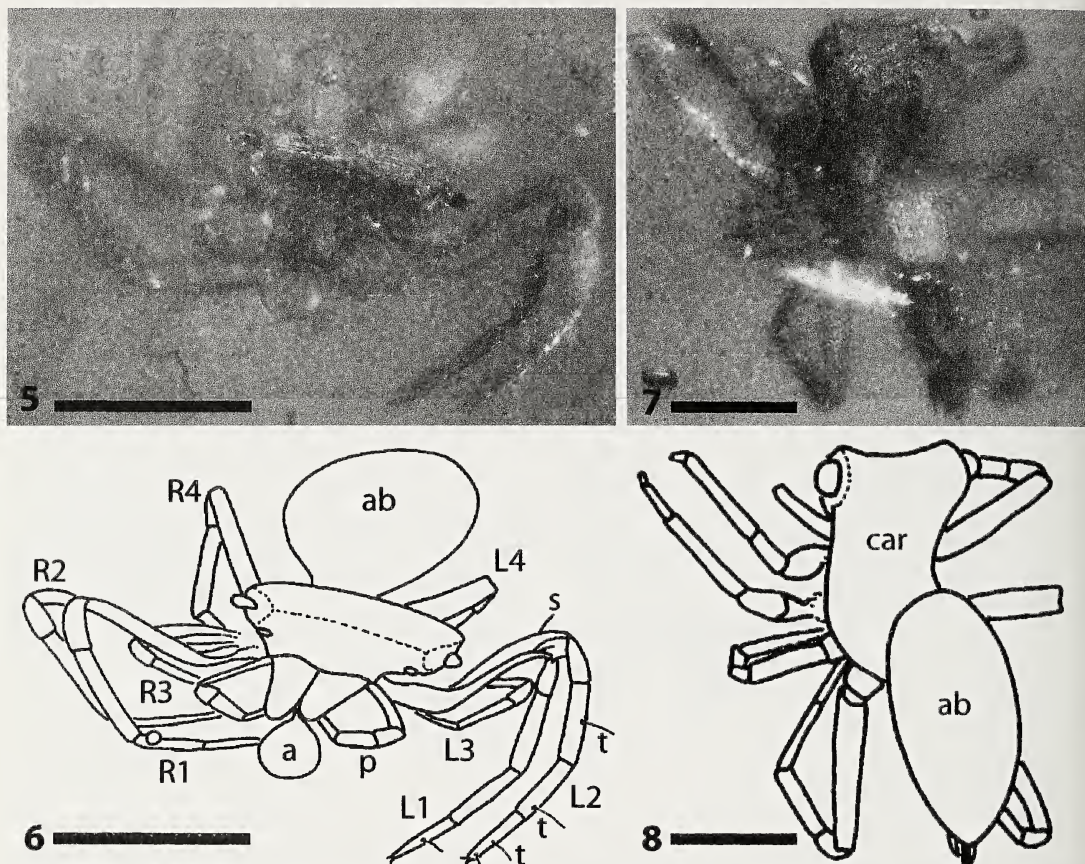
**Distribution.**—Fossil species in Cretaceous amber from Myanmar. Recent species not known.

*Burlagonomegops eskovi* new species  
Figs. 1–8

*Lagonomegopidae*: Grimaldi et al. 2002: 29, fig. 18e (AMNH BU-707).

**Material examined.**—Holotype juvenile, Burmese amber, MYANMAR, Kachin: Tanai Village (on Ledo Road 105 km NW of Myitkyna), 2000, by the Leeward Capitol Corporation (AMNH Bu-707). Paratype: 1 juvenile, same data as holotype (AMNH Bu-1353).





Figures 5-8.—*Burlagonomegops eskovi* new genus and species. Paratype, AMNH Bu-1353, juvenile, Burmese amber. 5, 6. anterior view. 7, 8. dorsal view. Scale lines = 0.5 mm.

**Etymology.**—The specific epithet is a patronym in honor of Dr. Kirill Eskov (Paleontological Institute, Moscow) in recognition of his contributions to paleoarachnology and his audible joy and excitement upon first viewing the paratype under a microscope.

**Diagnosis.**—As for genus.

**Description (based on both holotype and paratype).**—Body length 1.8; carapace 0.8 long, 0.5 wide between the eyes when viewed dorsally. With distinct, long setae, sides rounded in the thoracic region, cephalic region distinct and with a slightly procurved anterior edge (Figs. 3-4), lacking a fovea. Two large eyes, situated in flank positions anteriorly (Figs. 1-8). When viewed anteriorly, distance between clypeal margin and a hypothetical line joining these eyes at their centres 0.2; a second pair of smaller eyes are located midway between the large eyes and the end of the clypeal margin (Figs. 2, 6), width of clypeal

margin 0.4, with long, curved setae projecting inwards from both sides. Chelicerae twice as long as wide, with long setae projecting downwards, not possible to determine whether peg-teeth are present or absent. Sternum 0.4 long, 0.3 wide between coxae 2, truncate anteriorly and with sparse, long setae. Fang short, unmodified, labium as long as broad, maxillae longer than broad and converging. Opisthosoma oval (Figs. 3-4, 7-8), 1.0 long, 0.4 wide; spinnerets unmodified and in a compact group at the distal tip (Figs. 7-8).

Leg formula unknown because neither specimen is preserved in a manner conducive to making accurate measurements, all segments setose. Legs 1 and 2 appear approximately equal in length, 2.0, leg 4 may be slightly longer and leg 3 is distinctly shortest. Leg spines thin and weak, visible dorso-distally on femora 1, 2 and 4 and the patellae of the pedipalp and legs 1, 2 and 3. Trichoboth-



ria: tibia 1 with paired (tibiae 2–4 with at least one), each metatarsus with one long in the distal half and each tarsus with one long median and one short distal (Figs. 2, 6). Tarsi with three claws.

**Remarks.**—Although both preserved in Burmese amber, each specimen appears to have undergone different diagenetic/taphonomic processes, to such an extent that at first sight they appear to be quite different from one another. The best preserved specimen is the holotype, the paratype seems to have undergone some somatic distortion in carapace shape anteriorly and in the legs, which appear thin, stretched and twisted. In addition, the majority of setae have not been preserved in the paratype.

**Distribution and age.**—Burmese amber, Myanmar (Burma); Albion, Lower Cretaceous (Cruickshank & Ko 2003).

## DISCUSSION

The known geological range of lagonomegopids now spans approximately 25 Ma, from 100 Ma Burmese amber into the Campanian (Canadian amber; Penney 2004c). The younger end of the known range is 75 Ma, shortly before the Cretaceous–Tertiary (K/T) boundary dated at 65 Ma. This boundary marks the mass extinction event that wiped out the dinosaurs and numerous other groups. Spider inclusions in Tertiary ambers are extremely common and the lack of Lagonomegopidae in these fossil resins, when considered against their frequent occurrence in Mesozoic resins, suggests they may have become extinct during this event, in contrast to many other spider families which survived it (Penney et al. 2003). However, undiscovered extant species of Lagonomegopidae may exist, as was suggested by Eskov & Wunderlich (1995), but their absence in Tertiary resins makes this unlikely. It is more probable, given the general habitus and frequent occurrence of lagonomegopids in Cretaceous ambers that they occupied a similar niche to the Recent Salticidae (the most species-rich family today), which are extremely frequent in Tertiary ambers but have not been described from the Cretaceous. Thus, the lagonomegopids may represent a primitive lineage which gave rise to the Salticidae or they may have been ecologically replaced by them. The discovery of mature lagonomegopids with clearly visible genitalia

should help resolve this problem and confirm or reject their superfamilial placement in Palpimanoidea.

## ACKNOWLEDGMENTS

I thank D. Grimaldi of the American Museum of Natural History, New York for preparing and providing the Burmese and New Jersey amber specimens for research purposes and P. A. Selden for his comments on the manuscript. The Royal Society is thanked for a conference travel grant, the Leverhulme Trust for research funding and the conference organizers for hosting an excellent congress.

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## THE GENERIC RELATIONSHIPS OF THE NEW ENDEMIC AUSTRALIAN ANT SPIDER GENUS *NOTASTERON* (ARANEAE, ZODARIIDAE)

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**ABSTRACT.** A revision of the new endemic Australian genus *Notasteron* revealed two species, *Notasteron carmarvon* new species (male), *Notasteron lawlessi* new species (female, male). The genus is characterized by a strongly reticulated, shield-shaped sternum with steep lateral margins and a posteriorly situated boss. The male palp has a semicircular and undulated distal tegular apophysis and the female epigyne has long, convoluted copulatory ducts. Possible relationships of *Notasteron* with genera of the *Asteron* complex, *Habronestes*, *Hetaerica*, *Malinella* and *Storosa*, are analyzed with NONA and also reconstructed using the Hennigian method. The results indicate that the new genus does not belong to the *Asteron* complex but is the sister genus of *Hetaerica*. *Notasteron lawlessi* is quite common and occurs throughout the eastern part of Australia, whereas *N. carmarvon* is only found in the Carnarvon region of Western Australia.

**Keywords:** Taxonomy, new species, cladistics

The arachnid family Zodariidae is one of the most dominant ground-living spider families in Australia (Churchill 1998). Most species can be easily recognized by their bright yellow or orange spots on a dark brown abdomen and their annulated legs. With now 232 described and an estimated 350–400 total species, Australia has one of the richest known zodariid spider faunas worldwide. Rudy Jocqué's generic revision of the Zodariidae (1991) initiated intensive studies of the Australian zodariid fauna (Jocqué 1991, 1995a, b; Jocqué & Baehr 1992, 2001; Baehr & Jocqué 1994, 1996, 2000). With funding from the Australian Biological Resources Study Participatory Program, 130 additional new species, including this revision, were described within the last three years (Baehr & Jocqué 2001; Baehr 2003a, b, c, 2004a, b; Baehr & Churchill 2003).

The two species of the new genus *Notasteron* described here, were initially thought to belong to the *Asteron* complex because they share a similar abdominal pattern and the same general palp structure as the derived genera of the *Asteron* complex, *Basasteron* (Rainbow 1920), *Cavasteron* Baehr & Jocqué 2000, *Euasteron* Baehr 2003, *Holasteron* Baehr 2004a, *Masasteron* Baehr 2004b, *Minasteron* Baehr & Jocqué 2000 and *Spinasteron*

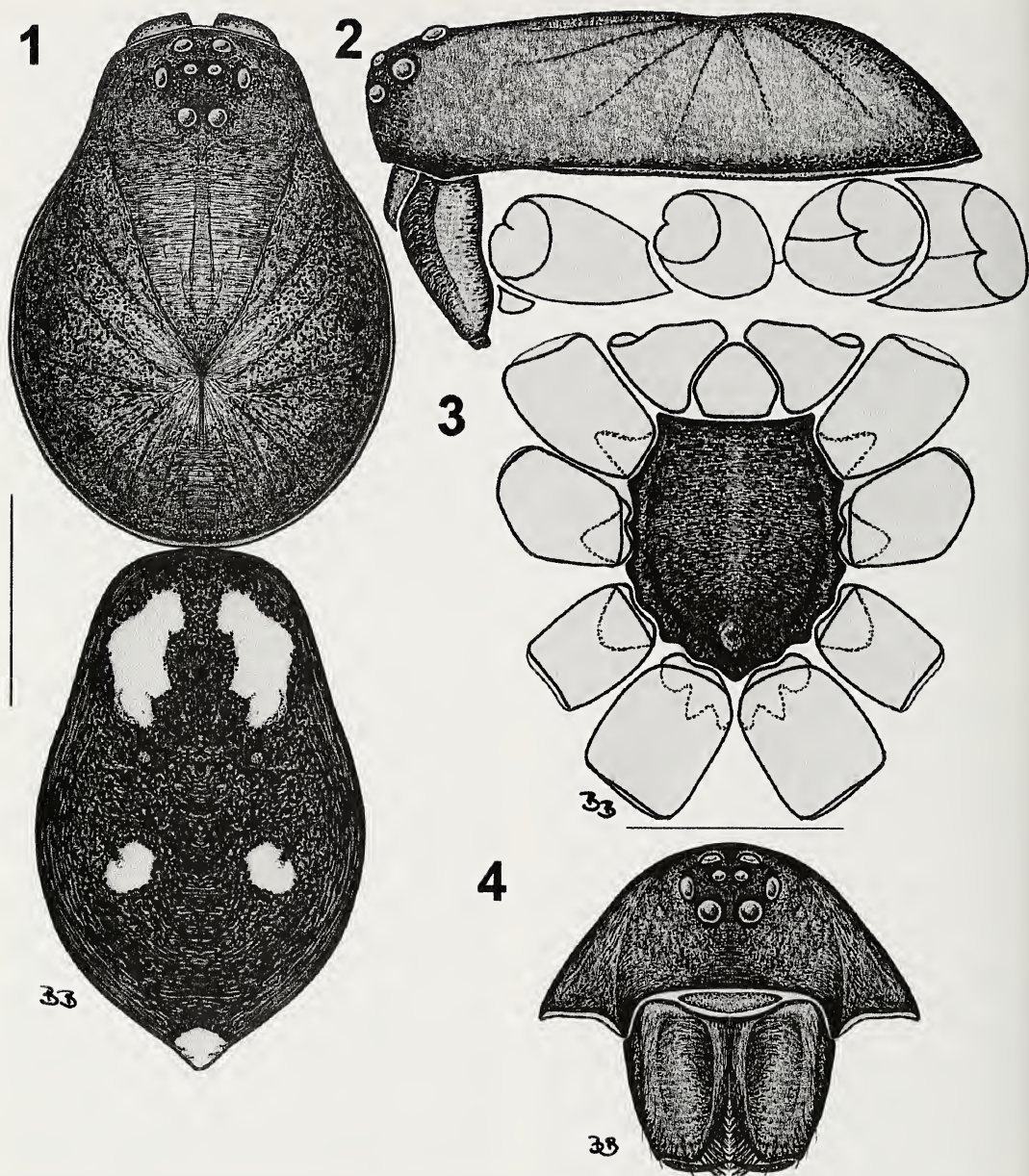
Baehr & Churchill 2003. These genera are characterized by a thin semicircular embolus and an enormous semicircular distal tegular apophysis (DTA). The peculiar structure of the distal tegular apophysis is unique within the Australian zodariids but it occurs also in *Tenedos* O.P.-Cambridge 1897 (Jocqué & Baert 2002), a large South American genus.

The use of a scanning electron microscope revealed significant differences in the structure of the sternum, the labium, the endites and the coxae between *Notasteron* and the *Asteron* complex. The sternum of the species in the *Asteron* complex is flat or only slightly convex, shiny, finely reticulated and has a smooth, rebordered margin (Fig. 11). The species of *Notasteron* have a strong reticulated sternum with a weak boss posteriorly and a steep lateral margin (Fig. 12). Species of the *Asteron* complex have a triangular labium, but it is more rectangular with a narrow base and a broadly rounded tip in *Notasteron*. The endites within the *Asteron* complex are triangular and medially straight whereas the *Notasteron* has medially concave endites. These characters are shared partly with *Hetaerica* Rainbow 1916 and *Storosa* Jocqué 1991 (Figs. 13, 14).

### METHODS

Descriptions are based on material stored in 70% ethanol. Epigynes were cleared in lactic



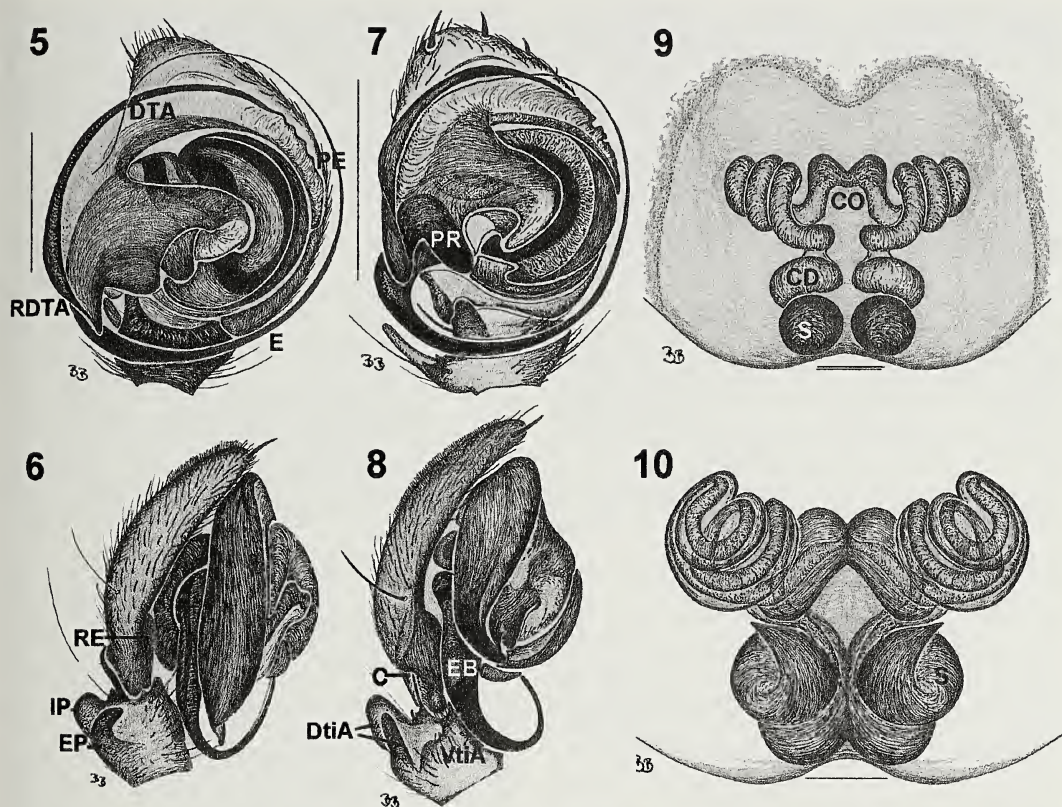


Figures 1–4.—*Notasteron lawlessi*. 1. body dorsal. 2, 4. carapace; 2. lateral; 4. frontal; 3. sternum and coxae. Scale bar = 1 mm.

acid. Descriptions were generated with the aid of Intkey (Dallwitz et al. 1998) and shortened where possible. Location data and maps were created with Biolink version 1.5 (CSIRO Entomology, Canberra, Australia; <http://www.biolink.csiro.au/>). Descriptions of spination and color patterns follow that in the revision of *Euasteron* (Baehr 2003a). Abbreviations of characters: ALE = anterior lateral eyes, AME = anterior median eyes, C = concavity on re-

trolateral part of cymbium, CL/CW = carapace length / width, CD = copulatory duct, CO = copulatory opening, DTA = distal tegular apophysis (in previous papers called dorsal tegular apophysis = conductor), DtiA = dorsolateral tibial apophysis, E = embolus, EB = embolus base, EP = external prong on dorso-retrolateral tibial apophysis, IP = internal prong on dorso-retrolateral tibial apophysis, PE = prolateral extension of DTA, PLE





Figures 5–10.—*Notasteron* spp., right male palps. 5, 7. ventral; 6, 8. lateral; 9, 10. epigyne. 9. ventral; 10. dorsal (cleared). 5, 6. *N. carnarvon*; 7–10. *N. lawlessi*. Scale bar = 0.5 mm (male palps), 0.1 mm (epigyne). Abbreviations: DTA = dorsal tegular apophysis; E = embolus; EP = external prong on dorso-retrolateral tibial apophysis (DtIA); IP = internal prong on dorso-retrolateral tibial apophysis (DtIA); PE = prolateral extension of DTA; PR = prong as ventral part of RDTA; RDTA = retrolateral extension of DTA; RE = retrolateral extension on cymbial flange; VtiA = ventral tibial apophysis.

= posterior lateral eyes, PME = posterior median eyes, PR = prong as ventral part of RDTA, RE = retrolateral extension on cymbial flange, RDTA = retrolateral extension of DTA, S = spermatheca, SL/SW = sternum length/width, VtiA = ventral tibial apophysis.

Abbreviations of institutions from which material was borrowed: Australian Museum, Sydney (AM); American Museum of Natural History, New York (AMNH); Museum Victoria, Melbourne (MV); South Australian Museum, Adelaide (SAM); Queensland Museum, Brisbane (QM); Western Australian Museum, Perth (WAM).

## SYSTEMATICS

Family Zodariidae Thorell, 1881

*Notasteron* new genus

**Type species.**—*Notasteron lawlessi* new species.

**Etymology.**—The generic name reflects the fact that *Notasteron* is not a genus of the *Assteron* complex, and is considered neuter in gender.

**Diagnosis.**—Species of *Notasteron* resemble those of *Hetaerica* in having a sternum with steep lateral margins and of *Storosa* in having a sternum with a posterior boss in males, but can be distinguished by the undulated prolateral part of DTA in the male palp (Figs. 5–8, 12) and the long convoluted epigynal ducts (Figs. 9, 10).

**Description.**—Medium sized spiders (4.80–5.70) with oval, roughly reticulated, laterally rebordered carapace, widest between coxae II and III, narrowed in front to about 0.53 of maximum width. Profile flattened, with the highest point behind fovea (Fig. 2). Color of carapace, sternum and chelicerae orange to sepia brown; endites and labium sepia



brown, distally white. Abdomen sepia brown; dorsally with two pairs of white patches on top and one above the spinnerets; ventrally dark brown. Legs brown. Eyes (Figs. 1, 2, 4) in three rows (2–4–2). ALE in first row, AME, PLE in second, PME third row. AME smallest. Clypeus curved downwards, height about 2.3 times the diameter of ALE. Chillum single. Chelicerae with longitudinal boss and lateral condyle, few setae in front and a dense row of setae on distal promargin, with one tooth on promargin (Fig. 4). Endites broad, median margin concave with anteromesal scopula, no serrula, labium inverted u-shaped, basally constricted. Sternum shield-shaped with straight anterior margin, roughly reticulated and punctated, posteriorly with weak boss, lateral margin steep (Fig. 12). Legs with few spines on pairs I and II, more numerous on III and IV. Metatarsal preening brush on metatarsi II and III weakly developed. Paired tarsal claws with eight teeth on inner side, unpaired claw toothless, on onychium. Abdomen oval with two sigilla. Anterior lateral spinnerets on common base, posterior median and posterior lateral spinnerets tiny, situated in one transverse row behind anterior spinnerets. Colulus represented by group of setae. Tracheal spiracle, tiny slit-like, covered by tiny sclerotized lip.

*Male palp* (Figs. 5–8): Cymbium with dorsal apical scopula, retrolaterally with straight, rectangular extension (RE). Cymbium base retrolaterally with concavity C (Fig. 8). DTA semicircular, distal part folded containing embolus, with short undulated PE; RDTA with well developed tip and prong. Embolus base hidden behind RDTA, embolus thin, semicircular. Tibia: VtiA bipartite, internal prong long needle-shaped, external part flat, rebordered along lateral margin; DtiA bipartite, IP spatulate as long as EP (Figs. 6, 8).

*Epigyne* (Figs. 9, 10): Epigyne with m-shaped copulatory openings, long convoluted copulatory ducts and small, globular spermathecae.

**Distribution.**—The two known species of *Notasteron* have a disjunct distribution. One species is quite common and occurs throughout the eastern part of Australia whereas the more derived species is only found in the Carnarvon region of Western Australia.

*Notasteron lawlessi* new species  
(Figs. 1–4, 7–10, 12, 16)

**Type material.**—Holotype male: AUSTRALIA: *Queensland*: Taroom, “Boggomoss” Station, 25°25’S, 150°01’E, 11 November 1996, P. Lawless, pitfall (QM S37401). Paratypes: AUSTRALIA: *Queensland*: 1 male, Barakula State Forest, Hellhole Creek, open woodland, 26°20’S, 150°42’E, 13–15 October 2004, C. Burwell, pitfall (QM S67697); 1 male, Taroom District, BS24, 25°25’S, 149°58’E, 12 November 1996–January 1997, P. Lawless, pitfall (QM S37214); 2 males, 2 females, Expedition Range National Park, ‘Amphitheatre’ yards, 440 m, 25°13’S, 149°01’E, 27 September 1997–4 March 1998, G. Monteith, D. Cook, pitfall (QM S44250, S44798); 1 female, Langlo Crossing, 3 km NW., 26°07’S, 145°39’E, 4 May 2001, G.B. Monteith, pyrethrum (QM S60615); 26 males, Lake Broadwater, via Dalby, site 2, 5, 9, 27°21’S, 151°06’E, 17 May 1985–25 February 1986, M. Bennie, pitfall (QM S47388–91, S47613–15); 2 males, same data (WAM T63078); 1 male, 1 female, Mount Gayndah, summit, 25°36’S, 151°32’E, 18 December 1998–27 January 1999, G. Monteith, pitfall (QM S55161); 1 male, 1 female, Mount Gayndah, 25°35’S, 151°32’E, 16 November 2000, N. Platnick, hand collecting (AMNH); 2 males, 3 females, Mount Gayndah, 25°36’S, 151°32’E, 21 November 1998, R. Raven, vibration (QM S51313); 3 males, Mount Stuart, 23°05’S, 148°41’E, 12 December 1999, D. Hannah, tree clearing, pitfall (QM S60741, S60743, S60744); 1 male, Mount Debatable, 1.5 km NE., 25°37’S, 151°34’E, 11 October–19 December 1998, G. Monteith, pitfall (QM S47569); 3 males, 1 female, Mount Pleasant, site 32.2, 24°52’S, 146°23’E, 30 October 1999, D. Hannah, tree clearing, pitfall (QM S60742, S60754); 3 males, Thylungra, site 3, 26°05’S, 143°27’E, October 1995, T. Churchill, pitfall (QM S60752); 9 males, Fairview, 24°19’S, 147°01’E, 6 November 1998, D. Hannah, tree clearing, pitfall (QM S60749, S60745); 4 males, Narrien, 22°53’S, 146°49’E, 1998, D. Hannah, tree clearing, pitfall (QM S60747); 4 males, Oakleigh, 26°51’S, 151°27’E, 1998, D. Hannah, tree clearing, pitfall (QM S60746); 1 male, Mulga gradient, pitfall traps 14–20, Site 5, October 1995, T. Churchill, pitfall (QM



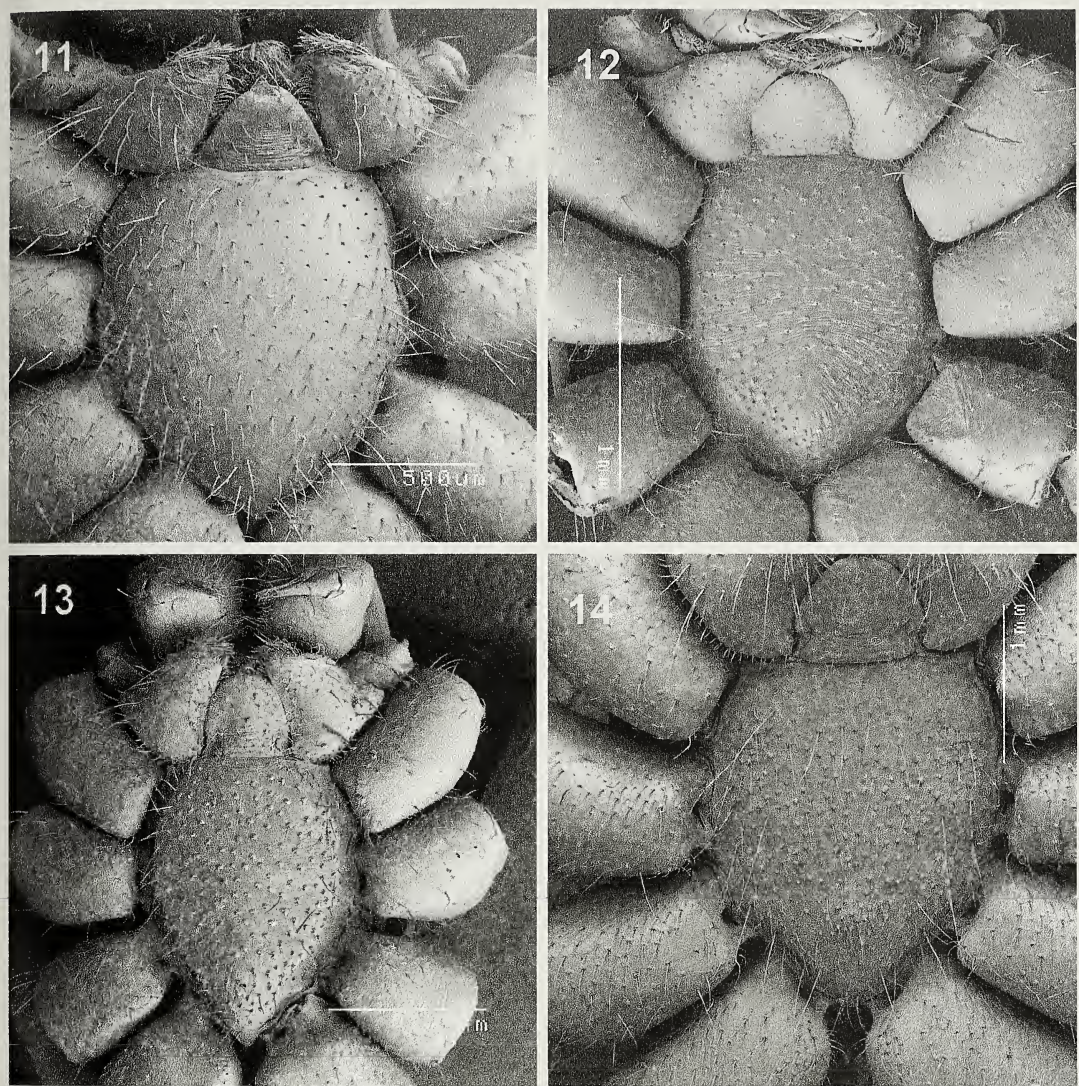


Figure 11–14.—*Sterna* and mouthparts. 11. *Masasteron queeslandicum*; 12. *Notasteron lawlessi*; 13. *Hetaerica scenica*; 14. *Storosa obscura*.

S60751); 13 males, Meta Park, 1998, tree clearing, pitfall (QM S60748); 1 female, Fleurs, site58/2, February 1999, tree clearing, pitfall (QM S60750); 3 females, Texas, 16 km S., 28°56'S, 151°08'E, 25 January 2002, B. Baehr, N. Platnick, R. Raven, vibration (QM S60616); 1 female, Wycheproof, 23°38'S, 146°51'E, 1998, tree clearing, pitfall (QM S60753); *New South Wales*: 1 female, Kelvin SF, 8 km N. of Kelvin, 30°45'S, 150°20'E, 23 November–14 December 2001, H. Doherty, M. Elliot, pitfall (AM KS82173); 3 males, 2 females, Dowe SF, 30°47'S, 150°30'E, 23 November–14 December 2001, L. Wilkie, H.

Smith, pitfall (AM KS82166, KS82168, KS82170–72); 1 male, 2 km from Tamworth on Tintinhull Rd, 31°04'S, 150°57'E, 15 November–6 December 2001, H. Doherty, M. Elliot, pitfall (AM KS82167); 1 male, between Kootingal and Tamworth, Crown Res. 200m past tip, 31°04'S, 151°02'E, 15 November–6 December 2001, G. Carter, pitfall (AM KS82169); 1 male, Gubatta, 33°36'S, 146°31'E, 6–14 December 1999, D. Driscoll, pitfall (QM S53897); 1 male, Morton Plains Station, 1.5 km NE. of Enngonia, 29°05'S, 146°12'E, 15 October 1991, R. Harris (SAM KS32557); 1 female, Pulletop, strip site 3P,



34°01'S, 146°04'E, 3–8 November 1999, D. Driscoll, pitfall (QM S53736); 1 male, Pulletop, reserve, 33°58'S, 146°05'E, 3–8 November 1999, D. Driscoll, pitfall (QM S53840); 9 males, 3 females, Pulletop, roadside, 34°01'S, 146°04'E, 12 October–8 November 1999, D. Driscoll, pitfall (QM S52523, S52642, S52732, S53778, S52919); 2 males, Pulletop site 10P, 33°55'S, 146°06'E, 12 October–8 November 1999, D. Driscoll, pitfall (QM S53279, S52817); 1 male, Rankins Springs, 33°45'S, 146°19'E, December 1999, D. Driscoll, pitfall (QM S45819); 3 males, Round Hill Nature Reserve site 1R, 33°03'S, 146°13'E, 19–23 December 1999, D. Driscoll, pitfall (QM S52587); 2 males, Round Hill Nature Reserve, site 4R, 32°59'S, 146°05'E, 2 November–23 December 1999, D. Driscoll, pitfall (QM S52700, S53115); 2 males, Round Hill Nature Reserve site 6R, 32°59'S, 146°03'E, 2–8 November 1999, D. Driscoll, pitfall (QM S52746); 3 males, Taleeban, 33°55'S, 146°28'E, 3–8 November 1999, D. Driscoll, pitfall (QM S53930, S52680); 1 male, 2 females, Taleeban site 4T, 33°57'S, 146°26'E, 23 February–18 October 1999, D. Driscoll, pitfall (QM S53101, S53039, S52131); 4 males, 2 females, Taleeban, roadside, 33°52'S, 146°25'E, 12 October–10 November 1999, D. Driscoll, Pitfall (QM S52650, S53127, S53128, S53531); 3 males, Taleeban, roadside site 8T, 33°53'S, 146°28'E, 1–10 November 1999, D. Driscoll, pitfall (QM S52661, S53753); 1 male, Taleeban site 10T, 33°57'S, 146°24'E, 3–10 November 1999, D. Driscoll, pitfall (QM S53761); *Victoria*: 2 males, Meringur, 5 km ESE., site 114, 34°24'S, 141°23'E, November 1985, A.L. Yen, drift fence pitfall (MV); *South Australia*: 3 males, 8 females, Danggali Conservation Park, Sandford Dam, 33°22'S, 140°54'E, 22–23 November 1996, D. Hirst, vibration (SAM NN17391–401); 3 males, 6 females, Danggali Conservation Park, 3 km N. Tomahawk Dam, 33°19'S, 140°43'E, 24–26 November 1996, J.A. Forrest, D. Hirst (SAM NN17402–09, NN17411); 1 male, same locality, 4 September 1996, D. Hirst (SAM NN17410); 1 male, 1 female, 8 km NNE. Mount Woodroffe, 26°15'S, 131°47'E, 13–17 October 1994, Pitjantjara Lands Survey, J.A. Forrest, pitfall (SAM NN 11435, NN11439); 1 male, Gluepot Res., 8.5 km W.-WNW. Gluepot Homestead, 33°44'S, 140°02'E, 26 November–6 Decem-

ber 2000, Gluepot survey, Sitella Camp (SAM NN17390); 2 males, 12.5 km E. Mitchell Nob, 26°08'S, 131°57'E, 20–21 October 1994, J.A. Forrest, pitfall (SAM NN11436–7); *Northern Territory*: 1 male, 1 female, Illamurta Spring, 24°18'S, 132°41'E, 26 March 1993, D. Hirst, pitfall (SAM NN17388–89); 1 female, Dangali Conservation Park, 1.5 km S. 3LO Dam, 33°17'S, 140°55'E March 2001, J.A. Forrest, D. Hirst, vibration (SAM NN17412).

**Etymology.**—The specific name is a patronym in honor of Phillip Lawless, formerly of the Queensland Museum, the collector of the holotype.

**Diagnosis.**—This species can be distinguished from the other species of the genus by the blunt tip of the RDTA in the male palp.

**Description.**—*Male (holotype)*: Total length 4.88. Cephalothorax 2.48 long; 1.80 wide; 0.80 high; cl/cw 1.37; sternum 1.20 long; 1.00 wide; sl/sw 1.20; abdomen 2.40 long; 1.52 wide. Color: body orange brown, to sepia brown, endites and labium distally white, abdomen dorsally with weak scutum and two pairs of white patches on top and with one above the spinnerets. Legs brown. Eyes: AME smallest; eye group width 0.50 of headwidth; AME 0.10; ALE 0.12; PME 0.12; PLE 0.12; AME-AME 0.04; AME-ALE 0.04; PME-PME 0.02; PME-PLE 0.10; ALE-PLE 0.04; eyes group AME-PME 0.34; AME-AME 0.24; PME-PME 0.26. Clypeus 0.28 high. Male palp (Figs. 7, 8): RDTA with blunt tip and strong prong, equal in length. DtiA IP spatulate as long as EP, EP peg-shaped.

*Female (paratype)*: Total length 5.48. Cephalothorax 2.60 long; 1.64 wide; 0.96 high; cl/cw 1.58; sternum 1.20 long; 1.08 wide; sl/sw 1.11; abdomen 2.88 long; 1.68 wide. Coloration as male, but no scutum. Eyes: AME smallest; eye group width 0.45 of headwidth; AME 0.09; ALE 0.12; PME 0.12; PLE 0.12; AME-AME 0.04; AME-ALE 0.04; PME-PME 0.04; PME-PLE 0.10; ALE-PLE 0.04; eyes group AME-PME 0.34; AME-AME 0.22; PME-PME 0.28. Clypeus 0.28 high. Legs: female palpal claw strong with eight teeth. Epigyne (Figs. 9, 10): CO m-shaped, half way between epigastric fold and end of epigyne. CD curled horizontally and vertically back to circular S.

**Variation.**—There is some variation in the body color from dark brown to light orange



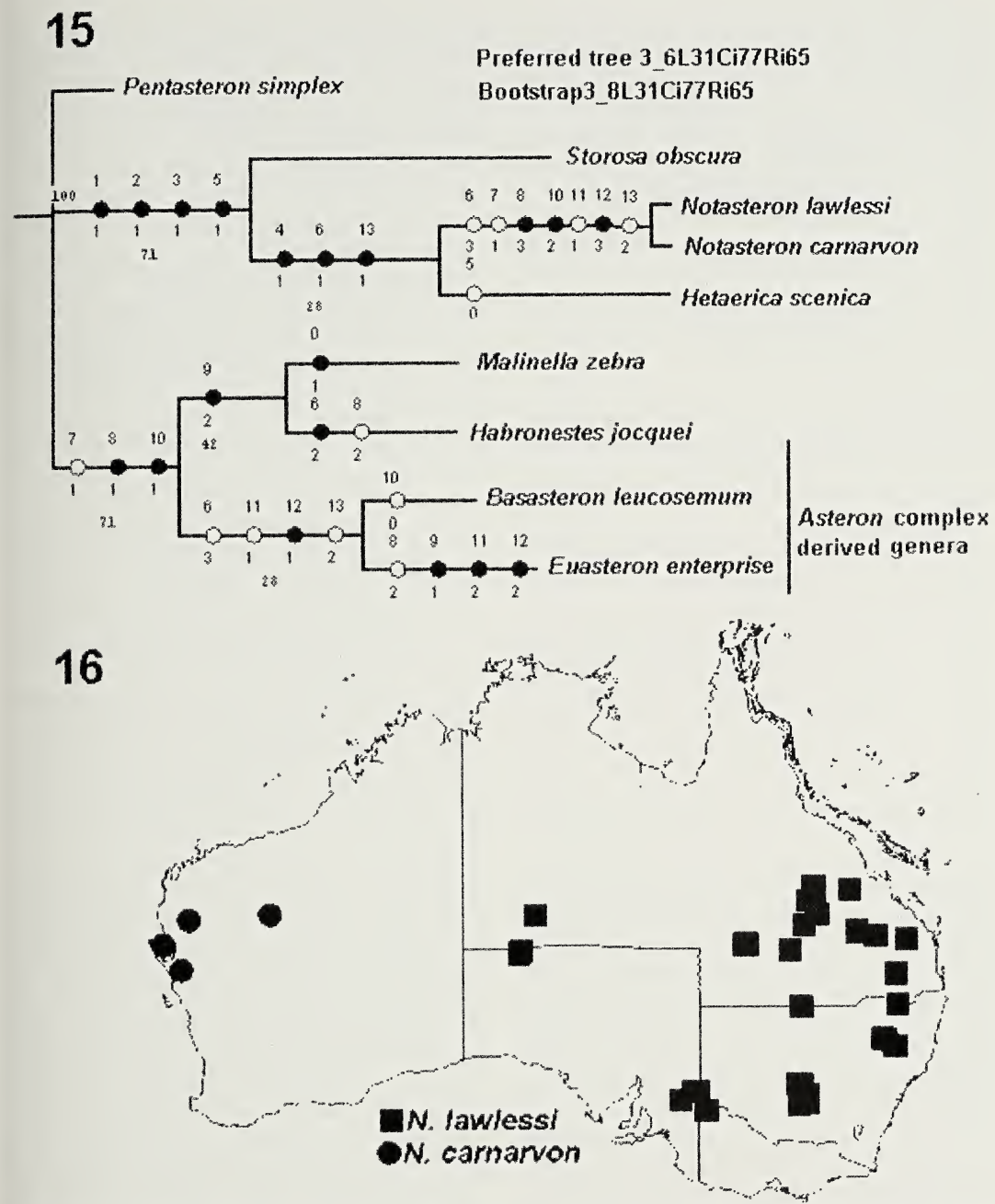


Figure 15, 16.—15. Phylogeny of some genera related to *Notasteron*, based on character matrix in Table 2. Cladogram of supposed relationships in sense of Hennig (1966), consistent with NONA (fast optimization). 16. Records of the genus *Notasteron* in Australia, rectangle *N. lawlessi*, circle *N. carnarvon*.

brown, but the color pattern of the abdomen is the same.

**Distribution.**—This species occurs in South Australia, southern part of Northern Territory, New South Wales, Victoria and Queensland (Fig. 16).

*Notasteron carnarvon* new species  
(Figs. 6, 16)

**Type material.**—Holotype male: AUSTRALIA: Western Australia: Francois Peron National Park, W. of Monkey Mia along road

Table 1.—Characters and character states scored for the cladistic analysis.

Character number	Character	Character state
0	AME size	0, smallest; 1, largest
1	Labium shape	0, triangular; 1, inverted u-shaped
2	Endites medial margin	0, straight; 1, concave
3	Sternum surface	0, smooth, shiny; 1, strongly reticulated, or/and punctated
4	Sternum profile	0, flat, rebordered; 1, elevated, with steep lateral margin (in males)
5	Sternum posteriorly	0, flat; 1, with posterior boss (in males)
6	Palp DTA shape	0, short; 1, cone-shaped, with enrolled lateral margin; 2, with stalk and enrolled tip; 3, semicircular with distinct RDTA and PE
7	Base of embolus	0, part of tegulum; 1, separated from tegulum as a chitinous plate
8	Base of embolus, shape	0, unmodified; 1, conical; 2, flattened; 3, hidden behind RDTA
9	Retrolateral cymbial flange (RE)	0, rectangular; 1, with rounded extension; 2, retrolateral concavity
10	TBE direction	0, pro-laterad; 1, baso-laterad; 2, retro-laterad
11	DTA, prolateral extension (PE) length	0, PE absent; 1, inside cymbium; 2, reaching tibia
12	Prolateral extension (PE) shape	0, PE absent; 1, about $\frac{1}{4}$ of circle; 2, about $\frac{1}{2}$ of circle; 3, about $\frac{1}{4}$ of circle lateral margin undulated
13	VTA	0, present; 1, reduced to a tiny spine; 2, absent

to Denham, 25°47'32"S, 113°41'37"E, 7 November 1998, J.M. Waldoock, vehicle vibration (WAM T54483). Paratypes: AUSTRALIA: *Western Australia*: Kennedy Range National Park, 24°31'25"S, 114°57'55"E, 14 January–7 April 1995, W. Muir, wet pitfall (WAM T54696); 3 males, Nerren Nerren Station, 27°03'S, 114°35'E, 11 January–11 May 1995, P. West et al., wet pitfall (WAM T44494); 1 male, same locality, 11 May–18 August 1995, N. Hall (WAM T54699); 1 male, same data (QM S67696); 1 male, Nerren Nerren Station, 27°03'24"S, 114°35'21"E, 25 August–16 October 1994, J.M. Waldoock et al., wet pitfall (WAM T44496).

**Etymology.**—The specific name is a noun in apposition taken from the region in which this species occurs.

**Diagnosis.**—This species can be distinguished from *N. lawlessi* by the sharp tip of RDTA in the male palp.

**Description.**—*Male (holotype)*: Total length 5.60. Carapace 3.00 long; 2.20 wide;

1.08 high; cl/cw 1.36; sternum 1.36 long; 1.16 wide; sl/sw 1.17; abdomen 2.60 long; 1.80 wide. Color: body sepia brown, endites and labium distally white. Abdomen dorsally with two pairs of white patches on top and one above the spinnerets. Legs brown. Eyes: AME smallest; eye group width 0.44 of headwidth; AME 0.11; ALE 0.14; PME 0.14; PLE 0.14; AME-AME 0.04; AME-ALE 0.04; PME-PME 0.04; PME-PLE 0.12; ALE-PLE 0.04; eyes group AME-PME 0.40; AME-AME 0.26; PME-PME 0.32. Clypeus 0.32 high. Male palp (Figs. 5, 6): RDTA with sharp tip and flattened prong. Embolus base flattened; DtiA IP spatulate as long as EP, EP bent ventrally. *Female*: Unknown.

**Distribution.**—Found only in the Carnarvon region of Western Australia (Fig. 16).

#### PHYLOGENETIC ANALYSIS

As the primary tool for the phylogenetic analysis, I used the methods originally proposed by Hennig (1966) and further explained



by Sudhaus & Rehfeld (1992, p.137). Only homologous characters were considered where I was able to determine plesiomorphic and apomorphic character states. I followed the technique of Watrous & Wheeler (1981), using an outgroup, preferably a sister taxon, to determine the polarity of the character states. Based on these character states, I attempted to deduce the phylogenetic history of the species-groups. The result of this phylogenetic analysis (sensu Hennig 1966) was tested with NONA version 2.0 (Goloboff 1997) using the heuristic search option and following settings: 5,000 random taxon addition replications (mult\*N), 5 starting trees per replication, and multiple tree-bisection-reconnection (TBR) branch swapping. The NONA bootstrap consensus tree was calculated with 1,000 replications, 10 search replications, and 5 starting trees per replication. I analyzed the same data set using unordered character states and fast optimization. Unsupported nodes were collapsed. The analysis is restricted to selected genera of the *Asteron* complex and the genera *Habronestes*, *Hetaerica*, *Notasteron* and *Storosa*. It is used here to define where *Notasteron* should be placed in the Zodariinae. The genera are represented by one species reflecting the “grundplan” in the sense of Hennig (1966) for the considered character states. Yeates (1995) called this the exemplar method. The species *Pentasteron simplex* Baehr & Jocqué 2001, *Basasteron leucosemum* (Rainbow 1920), *Habronestes jocquei* Baehr 2003, *Storosa obscura* Jocqué 1991 and *Hetaerica scenica* (Koch 1872) were chosen for the relatively primitive male palpal morphology of the considered genera. *Euasteron enterprise* Baehr 2003 was added as a representative of the putatively derived genus of the *Asteron* complex to see how robust the cladogram behaved. *Malinella zebra* (Thorell 1881), the only known Australian species from a paleotropical zodariid genus, was selected first as the outgroup taxon, then replaced by *Pentasteron simplex* Baehr & Jocqué 2001, the most basal representative of the analysis.

**Character assessment.**—The sternum, labium and endites provide few distinguishing characters which appear to be informative at the genus and higher level. The eye pattern and particularly the male palps provide synapomorphic features of high value for phylo-

Table 2.—Character matrix for species used in cladistic analysis.

Taxon	0–4	5–9	10–13
<i>Pentasteron simplex</i>	00000	00000	0000
<i>Basasteron leucosemum</i>	00000	03110	0112
<i>Euasteron enterprise</i>	00000	03121	1222
<i>Habronestes jocquei</i>	00000	02122	1000
<i>Malinella zebra</i>	10000	00112	1000
<i>Notasteron lawlessi</i>	01111	13130	2132
<i>Hetaerica scenica</i>	01111	01000	0001
<i>Storosa obscura</i>	01110	10000	0000

genetic examinations on species-group level. Derived characters of single species (autapomorphies, e.g., epigynes) are not discussed here. Characters and their states are listed in Table 1.

**Sternum:** The surface of the sternum is smooth and shiny (character 3/0), the profile is flat, the lateral margin is rebordered (character 4/0) in all species of the *Asteron* complex and in *Habronestes*. In contrast, all examined species of *Notasteron*, *Hetaerica*, and *Storosa* have a strongly reticulated and/or punctate sternum (character 3/1) with steep lateral margin in *Notasteron* and *Hetaerica* (character 4/1), and with a posterior boss in *Notasteron* and *Storosa* (character 5/1).

**Mouthparts:** Within the Zodariinae, the shape of the labium and the endites are distinguishing characters at the genus or higher level. All species of the *Asteron* complex and *Habronestes* possess a triangular labium (character 1/0) and endites with a straight medial margin (character 2/0). The labium of *Hetaerica* and *Storosa* is inverted u-shaped (character 1/1) and the endites of these genera as well as *Notasteron* are concave on the medial margin (character 2/1).

**Eyes:** In all Zodariinae, both eye rows are so strongly procurved that they appear to be in three rows (2–4–2): ALE in the first row, AME and PLE in the second row, and the third row consists only of PME (Figs. 1, 2, 4). In all *Notasteron*, *Hetaerica* and *Storosa* species, the AME are smaller than the other eyes. This is also the case for the “grundplan” species *Basasteron leucosemum*, *Pentasteron simplex*, *Habronestes jocquei* and *Euasteron enterprise* (character 0/0). In *Malinella zebra*, the AME are largest (character 0/1). The increase in size of the AME seems to be derived

but has presumably happened convergently quite frequently in different genera; e.g., in the genus *Habronestes* in the *Habronestes macedonensis* group (Baehr 2003c) and at least four times in the "derived" genera of the *Asteron* complex (some species of *Euasteron*, about half of the species of *Masasteron* and almost all species of *Spinasteron* and *Holasteron*).

**Male palp:** Most characters used in this phylogenetic study are taken from the male palp. Keeping in mind the primitive type of the male palp represented in *Storosa obscura* and *Pentasteron simplex*, the palps of *Notasteron* appear quite derived. The most spectacular change happens in the undulating of the semicircular DTA (character 12/3) and that the embolus base is hidden under the RDTA (character 8/3). The most plesiomorphic short and membranous DTA and a short straight embolus occur in *Storosa obscura* and *Pentasteron simplex* (character 6/0) whereas a cone-shaped DTA with an enrolled margin is synapomorphic for all *Hetaerica* species (character 6/1). The slender stalk-like DTA with an enrolled distal tip is unique for all *Habronestes* species (character 6/2). The main synapomorphy for the genus *Notasteron* and the derived genera of the *Asteron* complex (*Basateron*, *Cavasteron*, *Euasteron*, *Holasteron*, *Minasteron*, *Spinasteron*, *Tropasteron* and *Masasteron*) is the large semicircular DTA with marginal fold, well developed retrolateral-(RDTA) and prolateral extension (PE) (character 6/3). As this kind of DTA is unique in the Australian Zodariinae, it could be thought that the above-mentioned derived genera of the *Asteron* complex and *Notasteron* are monophyletic. The base of the embolus is separated from the tegulum in the genera *Notasteron* and *Habronestes*, and in all derived genera of the *Asteron* complex. Whereas in *Habronestes* and in the *Asteron* complex, the embolus base is uncovered it is hidden in *Notasteron* (characters 7/1, 8/3). The position of the transbasal area of the embolus (TBE) provides a derived character state for the genus *Notasteron* (character 10/2). The retrolateral cymbial flange (RE) is rectangular and straight in the basal condition (character 9/0) as for *Notasteron*, *Storosa*, *Hetaerica*, *Pentasteron*, *Basasteron* but has a deep groove (character 8/2) as a synapomorphy for all *Habronestes* species. In the derived genera of the

*Asteron* complex the flange consists of a rounded extension (character 8/1).

**Results.**—The cladistic analysis of the data matrix (Table 2) with NONA including 14 characters and seven taxa resulted in three most parsimonious trees (length 26 steps, CI = 80, RI = 68). *Euasteron enterprise* was added to the data matrix representing the more derived genera of the *Asteron* complex. In this case, six most parsimonious trees were found (length 31 steps, CI = 77, RI = 65). In all trees, *Notasteron* was matched with only three of eight taxa. The pair *Notasteron*-*Basasteron* is based exclusively on the advanced male palp character states as synapomorphies. The sister-group constellation *Notasteron*-*Storosa* is based on the sternum with posterior boss taken as a synapomorphy (5/1). From the analyses; phylogenetic analysis in the sense of Hennig, the cladistic analysis with 7 taxa and 8 taxa, and the bootstrap ("majority rules"), the congruent tree in all was taken as the preferred tree (Fig. 15). The resulting tree shows that *Notasteron* is the sister genus of *Hetaerica* considering the somatic characters of the sternum, the endites and the labium as synapomorphic character states of the genera *Storosa*, *Hetaerica* and *Notasteron*, and the steep lateral margin as the main synapomorphic character state for *Hetaerica* and *Notasteron*.

**Biogeography.**—The Zodariidae are ground dwelling spiders that are not known to disperse aerially. The genus *Notasteron* includes only two species to date. Both species were found in a disjunct distribution pattern. The basal species, *N. lawlessi*, is quite common in the southern and eastern part of Australia (Fig. 16), like the most plesiomorphic species of the *Asteron* complex (*Pentasteron simplex*, *Basasteron leucosemum* and *Euasteron enterprise*); whereas the derived species, *Notasteron carnavon*, is only found in the Carnarvon region of Western Australia.

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## TARSAL SCOPULA SIGNIFICANCE IN ISCHNOCOLINAE PHYLOGENETICS (ARANEAE, MYGALOMORPHAE, THERAPHOSIDAE)

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**ABSTRACT.** Tarsal scopula condition and carapace length were studied for eighteen Ischnocolinae species. For cladistic analysis a matrix of 20 terminals and 30 characters of representatives of Ischnocolinae, Theraphosinae, Aviculariinae, Harpactirinae and Trichopelmatinae were analyzed using Nona 2.0 computer software. The matrix was analyzed in four different ways: 1. each tarsal scopula (legs I–IV) coded as separate characters; 2. one character with six ordered states; 3. one character with six independent states; 4. without tarsal scopula character. The first two matrices result in one tree with the same indices ( $L = 72$ ;  $CI = 0.54$ ;  $RI = 0.74$ ) and topology: Part of Ischnocolinae is monophyletic (*H. rondoni*(*S. longibulbi*(*I. algericus*+*Catumiri*))) and the other representatives (*Oligoxystre* and Genus 1) form a distinct monophyletic group with Theraphosinae, Harpactirinae and Aviculariinae. There are no homoplasies in tarsal scopula evolution in the second cladogram. The other two cladograms show less resolution for the Ischnocolinae than the two first cladograms. The tarsal scopula condition appears to have no relation to spider size ( $t = -0.80433$ ;  $P = 0.438247$ ) and should be used in phylogenetic analysis of Ischnocolinae because it provides information on the character variability within the subfamily.

**Keywords:** Phylogeny, South America, cladistics

The condition of the tarsal scopula has had an important role in the systematics of the Ischnocolinae Simon 1892. The scopula shows ontogenetic differentiation, being divided in all juvenile Theraphosidae and becoming entire in adults of some groups (Pocock 1897; Gerschman de Pikelin & Schiapelli 1973; Pérez-Miles, 1994). The condition of the tarsal scopula has been considered a good taxonomic tool and has already been used to diagnose genera and species groups in Theraphosidae. Its use in phylogenetics is questionable since, within the Theraphosinae, the presence of a divided scopula is related to small sized species (Pérez-Miles 1994). Characterized as theraphosids with a divided tarsal scopula (plesiomorphic state), Ischnocolinae is considered a paraphyletic group. Ischnocolinae is the subfamily of Theraphosidae Thorell 1869 that shows the broadest geographic distribution, with species occurring in northern, central and eastern Africa, Seychelles, the Middle-East, the Mediterranean region, central and south Americas and the Antilles (Smith 1990; Rudloff 1997; Vol 2001). Considering that Ischnocolinae was proposed as a

subfamily based on a plesiomorphic character state (divided tarsal scopula), the situation of the group's systematics is very confusing. Raven (1985) considered Ischnocolinae a paraphyletic group that should have been revised at the generic level and grouped into monophyletic units. However, since the description of the type-genus *Ischnocolus* Ausserer 1871, only a few genera have been revised. Gerschman de Pikelin & Schiapelli (1973) revised the subfamily as a whole but of the 42 genera included in this study, only 10 are in fact Ischnocolinae representatives. The remaining 12 were subsequently synonymized or transferred to other families and subfamilies. Rudloff (1997) revised the genus *Holothela* Karsch 1879 but did not present a diagnosis of the genus and its species; the identification key does not include all the species and the structures are poorly illustrated. Smith (1990) published a taxonomic revision of European and African Ischnocolinae and presented descriptions and diagnoses for all genera.

For over a century, the tarsal scopula state “divided by a longitudinal band of setae” was used in Theraphosidae taxonomy (Pérez-Miles



1994). Gerschman de Pikelin & Schiapelli (1973), following Ausserer (1871), considered the tarsal scopula condition an important taxonomic character and stated that the divided tarsal scopula is present in all juvenile theraphosids. Juvenile Theraphosinae Thorell 1870 have divided tarsal scopulae that become entire in the adult stage, in Ischnocolinae the scopulae remain divided into adulthood (Pocock 1897; Gerschman de Pikelin & Schiapelli 1973; Pérez-Miles 1994). Although this ontogenetic differentiation was detected, the divided condition continued to be used causing the inclusion of juvenile Theraphosinae within Ischnocolinae. This problem remained unresolved until Raven (1985) considered Ischnocolinae a paraphyletic group that presents poorly developed tarsal scopulae. The tarsal scopula as a phylogenetic character was used for the first time by Pérez-Miles (1992) in a preliminary cladistic analysis of the subfamily Theraphosinae. In this paper he shows that the entire tarsal scopula is synapomorphic for some genera of this subfamily. Later, Pérez-Miles (1994) discussed the value of the tarsal scopula in Theraphosinae systematics and concluded that the scopula condition is related to spider size, although some exceptions exist. Considering that the role of the tarsal scopula in Theraphosidae systematic remains obscure, the goal of this study is to vary the use of the character "tarsal scopula" in a phylogenetic analysis for Ischnocolinae and discuss the results.

## METHODS

The material examined belongs to the following institutions: Instituto Butantan, São Paulo (IBSP); American Museum of Natural History, New York (AMNH); Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires (MACN); Museo de la Plata, La Plata (MLP); Museu de Zoologia, Universidade de São Paulo, São Paulo (MZSP); Zoological Museum University of Copenhagen (ZMUC); Museu Paraense Emílio Goeldi, Belém (MPEG).

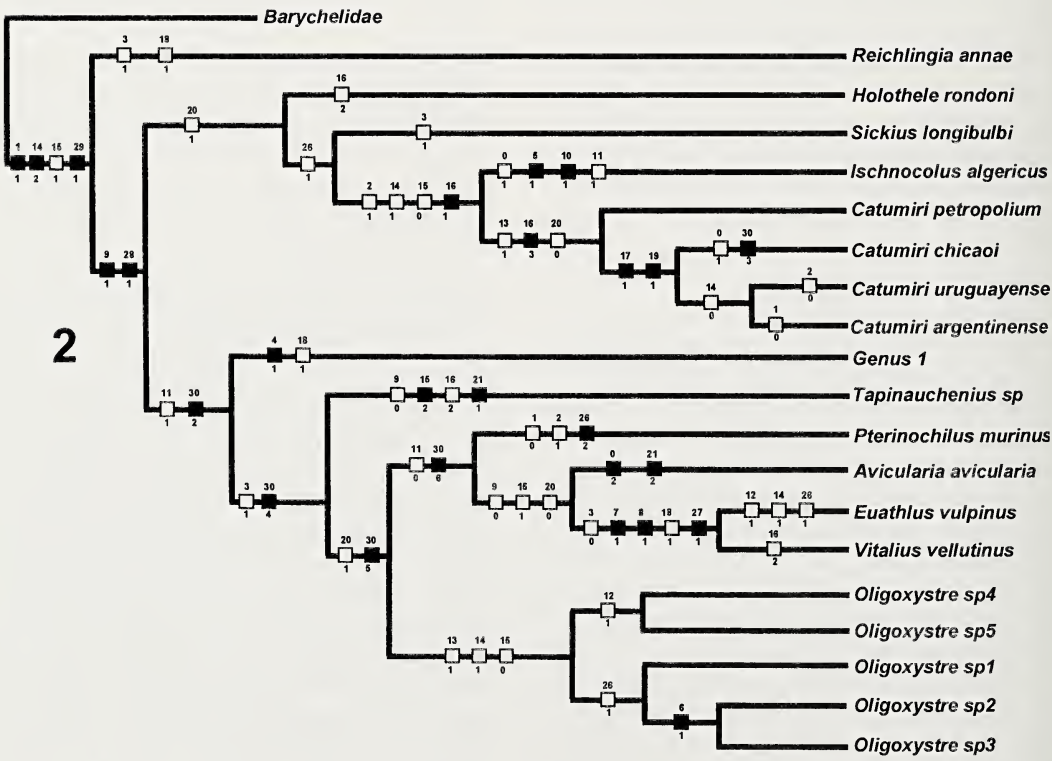
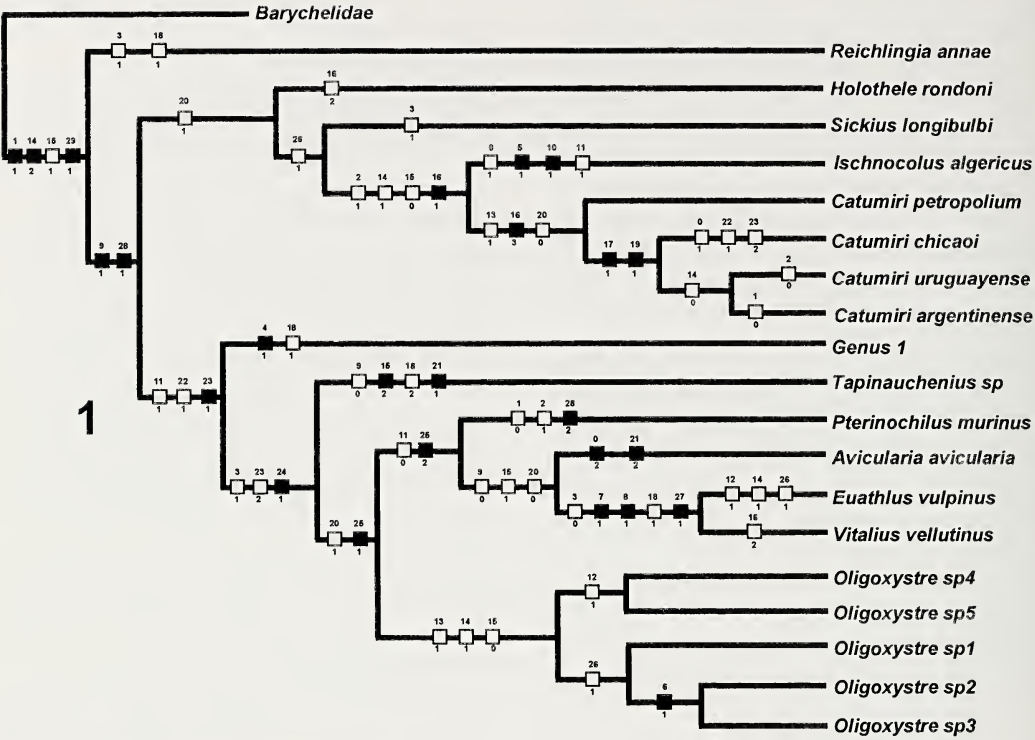
Tarsal scopula condition was observed under a stereomicroscope. Following Pérez-Miles (1994), a few isolated long and thin hairs in the tarsal scopula were not considered divided. Carapace length was used to estimate spider size. Below is a list of Ischnocolinae

species used for tarsal scopulae condition and carapace length:

- Holothele rondoni* (Lucas & Bücherl 1972): 1 ♂, Apíacas, Mato Grosso, Brazil (MZSP 18046); 1 ♂, Apíacas, Mato Grosso, Brazil (MZSP 18038); 1 ♂, Manicoré, Amazonas, Brazil (MZSP 18990). *Sickius longibulbi* Soares & Camargo 1948: 4 ♂, Itirapina, São Paulo, Brazil (MZSP 22756). Genus 1: 3 ♂, Colinas do Sul, Serra da Mesa, Goiás, Brazil (MZSP 18992). *Catumiri petropolium* Guadanucci 2004: 1 ♂, Petrópolis, Rio de Janeiro, Brazil (IBSP 8596). *Catumiri chicoai* Guadanucci 2004: 1 ♂, Una, Bahia, Brazil (IBSP 9514). *Catumiri uruguayense* Guadanucci 2004: 1 ♂, Lavalleja, Águas Blancas, Uruguay (IBSP 9491). *Catumiri argentinense* (Mello-Leitão 1941): 1 ♂, Jujuy, Yuto, El Pantanoso, Argentina (MACN 6424). Genus 2, sp. 1: 3 ♂, Jaraguá, Goiás, Brazil (MPEG 1677). Genus 2, sp. 2: 1 ♂, Serra Norte, Pará, Brazil (MPEG 1678). Genus 2, sp. 3: 1 ♂, Ilha Marajó Breves, Pará, Brazil (MPEG 1679). Genus 2, sp. 4: 1 ♂ (IBSP 11083), 1 ♂ (IBSP 11086), 1 ♂ (IBSP 11087), Pimenta Bueno, Rondônia, Brazil; 1 ♂, Mineiros, Goiás, Brazil (IBSP 8070). Genus 2, sp. 5: 1 ♂, Linhares, Espírito Santo, Brazil (IBSP 8654); 1 ♂, Linhares, Espírito Santo, Brazil (IBSP 7987); 1 ♂, Porto Seguro, Bahia, Brazil (IBSP 11084); 1 ♂, Ilhéus, Bahia, Brazil (IBSP 11085). *Oligoxystre* new species 1: 1 ♂ (IBSP 9488), 1 ♂ (IBSP 9489), 1 ♂ (IBSP 9486), 1 ♂ (IBSP 9484), Central, Bahia, Brazil.

**Cladistic analysis.**—The cladistic analysis was carried out using Nona version 2.0 (Goloboff 1993). Search strategy was mult\* with 100 replications. The data matrix included 20 terminal taxa and 30 characters and was constructed with NDE (Nexus Data Editor) version 0.5.0 (Page 2001). The out-group was chosen based on the phylogenetic relationships of Mygalomorphae presented by Goloboff (1993). In order to avoid an excess of missing entries, we preferred used a Barychelidae Simon 1889 rather than a Paratropididae Simon 1889 as the out group, since the last family presents some incomparable characters with Theraphosidae. Character polarity was read straight from the preferred cladogram following Nixon & Carpenter (1993).

Below is a list of species used in the cladistic analysis:



Figures 1–2.—Relationship hypothesis between Ischnocolinae and other Theraphosidae groups. 1. (L = 72; CI = 0.54; RI = 0.74). Tarsal scopula coded in four characters (22–25), one for each leg. 2. (L = 72; CI = 0.54; RI = 0.74). Tarsal scopula coded as one character with six ordered states.



Table 1.—Matrix composed of 20 terminals and 31 characters.

	Characters																															
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	
Barychelinae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Reichlingia annae</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	2	1	0	—	1	0	0	0	0	0	0	0	0	0	0	1	0	
<i>Holothele rondoni</i>	0	1	0	0	0	0	0	0	0	1	0	0	0	0	2	1	2	0	0	0	1	0	0	0	0	0	0	0	1	1	0	
<i>Sicktus longibulbi</i>	0	1	0	1	0	0	0	0	0	1	0	—	—	0	2	1	0	—	0	0	1	0	0	0	0	0	1	0	1	1	0	
<i>Ischnothele algericus</i>	1	—	—	0	—	1	0	0	0	1	1	1	0	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	1	1	0	
<i>Catumiri petropo-</i> <i>lium</i>	0	1	1	0	0	0	0	0	0	1	0	0	0	1	1	0	3	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0
<i>Catumiri chicao</i>	1	—	—	0	—	0	0	0	1	0	?	?	?	1	1	0	3	1	0	1	0	0	1	2	0	0	1	0	1	1	1	3
<i>Catumiri uruguay-</i> <i>ense</i>	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	3	1	0	1	0	0	0	0	0	0	1	0	1	1	1	0
<i>Catumiri argenti-</i> <i>nense</i>	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	3	1	0	1	0	0	0	0	0	0	0	1	0	1	1	0
Genus 1	0	1	0	0	1	0	0	0	0	1	0	1	0	0	2	1	0	—	1	0	0	0	1	1	0	0	0	0	0	1	1	2
<i>Tapinauch</i> sp.	0	1	0	1	0	0	0	0	0	0	1	0	0	0	2	2	2	0	0	0	0	1	1	2	1	0	0	0	1	1	4	
<i>Pterinochilus muri-</i> <i>nus</i>	0	0	1	1	0	0	0	0	0	1	0	0	0	0	2	1	0	—	0	0	1	0	1	2	1	2	1	2	0	1	1	6
<i>Avicularia avicularia</i>	2	—	0	1	0	0	0	0	0	0	0	0	0	0	2	1	0	—	0	0	0	2	1	2	1	2	0	0	1	1	6	
<i>Euathlus vulpinus</i>	0	1	0	0	0	0	0	1	1	0	0	0	1	0	1	1	0	—	1	0	0	0	1	2	1	2	1	1	1	1	6	
<i>Vitalius vellutinus</i>	0	1	0	0	0	0	0	1	1	0	0	0	0	0	2	1	2	0	1	0	0	0	1	2	1	2	0	1	1	1	6	
<i>Oligoxistre</i> sp. 4	0	1	0	1	0	0	0	0	0	1	0	1	1	1	1	0	0	—	0	0	1	0	1	2	1	1	0	0	1	1	5	
<i>Oligoxistre</i> sp. 5	0	1	0	1	0	0	0	0	0	1	0	1	1	1	1	0	0	—	0	0	1	0	1	2	1	1	0	0	1	1	5	
<i>Oligoxistre</i> sp. 1	0	1	0	1	0	0	0	0	0	1	0	1	0	1	1	0	0	—	0	0	1	0	1	2	1	1	0	0	1	1	5	
<i>Oligoxistre</i> sp. 2	0	1	0	1	0	0	1	0	0	1	0	1	0	1	1	0	0	—	0	0	1	0	1	2	1	1	1	0	1	1	5	
<i>Oligoxistre</i> sp. 3	0	1	0	1	0	0	1	0	0	1	0	1	0	1	1	0	0	—	0	0	1	0	1	2	1	1	1	1	0	1	1	5

BARYCHELIDAE: *Reichlingia annae* (Reichling 1997): 1 ♂, 1 ♀, New River Lagoon, Orange Walk, Belize (AMNH).

THERAPHOSIDAE: *Avicularia avicularia* (Linnaeus 1758) (Aviculariinae): 1 ♂, Jacaré, Rio Trombetas, Oriximiná, Pará, Brazil (MZSP 5687); 1 ♀, Jacaré, Rio Trombetas, Oriximiná, Pará, Brazil (MZSP 5687).

*Euathlus vulpinus* (Karsch 1880) (Theraphosinae): 5 ♂, Osorno, Chile (IBSP 3817-A); 4 ♀, Osorno, Chile (IBSP 3817-B).

*Catumiri petropolium* Guadanucci 2004 (Ischnocolinae): 1 ♂, Petrópolis, Rio de Janeiro, Brazil (IBSP 8596); 1 ♂, Petrópolis, Rio de Janeiro, Brazil (IBSP 8606).

*Catumiri chicao* Guadanucci 2004 (Ischnocolinae): 1 ♂, Una, Bahia, Brazil (IBSP 9514); 1 ♀, Una, Bahia, Brazil (IBSP 9514).

*Catumiri uruguayense* Guadanucci 2004 (Ischnocolinae): 1 ♂, Lavalaja, Águas Blancas, Uruguay (IBSP 9491); 1 ♀, Lavalaja, Águas Blancas, Uruguay (IBSP 9507).

*Catumiri argentinense* (Mello-Leitão 1941) (Ischnocolinae): 1 ♂, Jujuy, Yuto, El Pantanoso, Argentina (MACN 6424); 1 ♀, Catamarca, Argentina (MLP 14608).

Genus 1 (Ischnocolinae): 1 ♂, Fazenda Sandoval, Porto Nacional, Tocantins, Brazil (IBSP 8585); 1 ♀, Fazenda Sandoval, Porto Nacional, Tocantins, Brazil (IBSP).

*Holothele rondoni* (Lucas & Bücherl 1972) (Ischnocolinae): 1 ♂, Apiácas, Mato Grosso, Brazil (MZSP 18046); 1 ♀, Tucuruí, Pará, Brazil (IBSP).

*Ischnocolus algericus* Thorell 1875 (Ischnocolinae): 1 ♂, 1 ♀, El Araish, Morocco (ZMUC 620, 628).

*Oligoxystre* new species 1 (Ischnocolinae): 1 ♂, Central, Bahia, Brazil (IBSP 9487); 1 ♀, Toca da Esperança, Jussara, Bahia, Brazil (IBSP 8549).

*Oligoxystre* new species 2 (Ischnocolinae): 1 ♂, Chapada dos Guimarães, Mato Grosso, Brazil (IBSP 9495); 1 ♀, Chapada dos Guimarães, Mato Grosso, Brazil (IBSP 9504).

*Oligoxystre* new species 3 (Ischnocolinae): 1 ♂, São Domingos, Goiás, Brazil (IBSP 8625); 1 ♀, Serra da Mesa, Minaçu, Goiás, Brazil (IBSP 9467).

*Oligoxystre* new species 4 (Ischnocolinae): 1 ♂, Tucuruí, Pará, Brazil (IBSP 9459); 1 ♀, Tucuruí, Pará, Brazil (IBSP 7936).

*Oligoxystre* new species 5 (Ischnocolinae): 1 ♀, Toca da Esperança, Central, Bahia, Brazil (IBSP 8553).

*Pterinophilus murinus* Pocock 1897 (Harpactirinae): 1 ♂, Africa (IBSP); 1 ♀, Kenya (IBSP).

*Sickius longibulbi* Soares & Camargo 1948 (Ischnocolinae): 1 ♂, Parnaíba, Mato Grosso do Sul,

Brazil (IBSP 8019); 1 ♀, Votuporanga, São Paulo, Brazil (IBSP 8693).

*Tapinauchenius* sp. (Aviculariinae): 1 ♂, Tucuruí, Pará, Brazil (IBSP 4925-A); 1 ♀, Rio Marupí, Pará, Brazil (IBSP 4676).

*Vitalius vellutinus* (Mello-Leitão 1923) (Theraphosinae): 1 ♂, Porto Cabral, Rio Paraná, Teodoro Samapiao, São Paulo, Brazil (MZSP 14953); 1 ♀, Teodoro Samapiao, Porto Cabral, Rio Paraná, Teodoro Sampaio, São Paulo, Brazil (MZSP 3150).

## CLADISTIC ANALYSIS

Below is a list of the characters used to construct the data matrix. The matrix was analyzed in four different ways: 1. tarsal scopula of each leg was coded as a separate character (characters 22–25) and these were treated as ordered; 2. the four tarsal scopula were coded as a single character with six ordered states (character 30); 3. the four tarsal scopula were coded as a single character with six independent states (character 30); 4. the character(s) of the tarsal scopula were deactivated in the matrix. The optimization option was ACCT-RAN. Abbreviations: L = length of character; CI = consistency index; RI = retention index.

**0. Male tibial spur (L = 3; CI = 0.66; RI = 0).**—0, present; 1, absent; 2, present, formed by thick spines. The great diversity of male tibial spur morphology might be related to reproductive isolation. The tibial spur is the first structure that touches the female and could act as a mechanism for the female to recognize a conspecific male (Coyle 1985; Eberhard 1985; Jackson & Pollard 1990). Since the structures that compose the tibial spur are under independent evolution, the “tibial spur” is coded in three different characters.

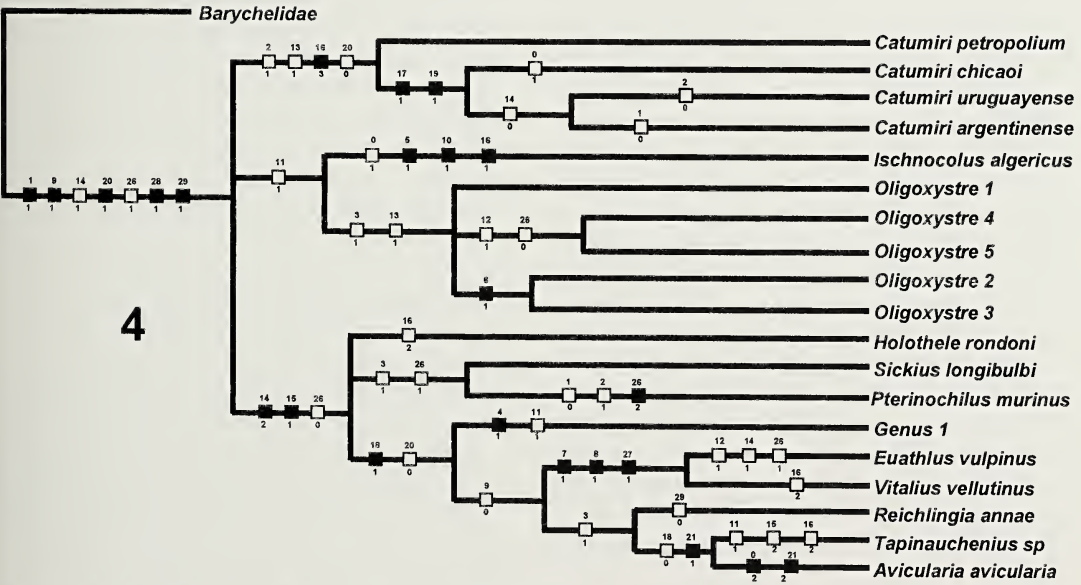
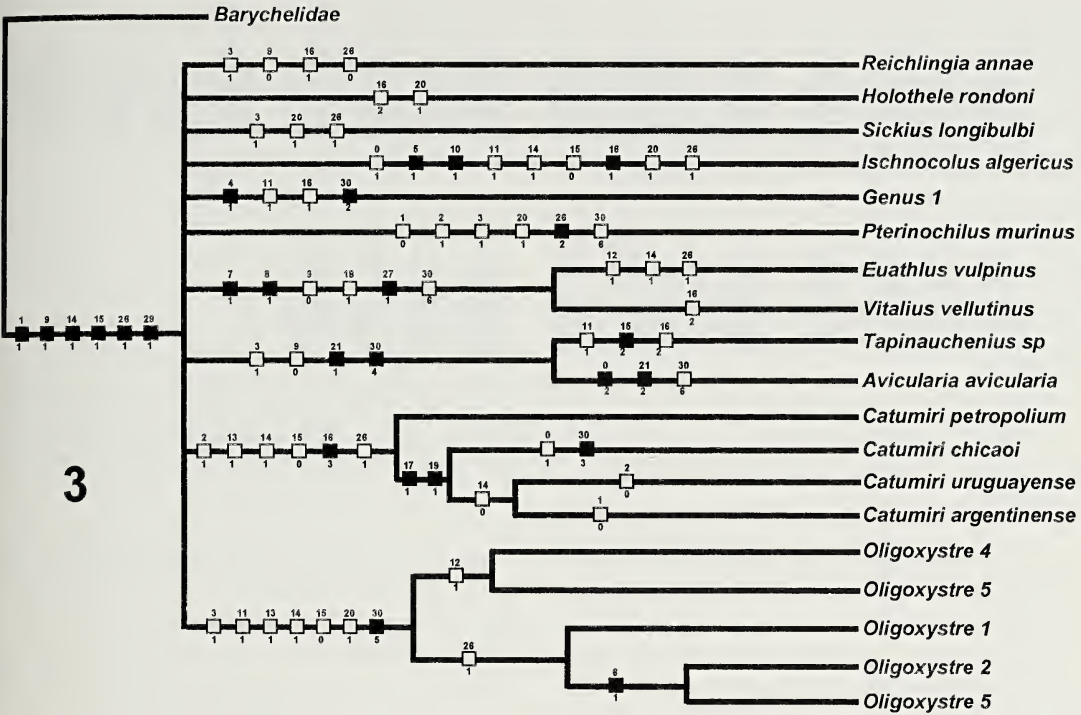
**1. Apical megaspine in the tibial spur (L = 3; CI = 0.33; RI = 0).**—0, present; 1, absent.

**2. Prolateral branch of tibial spur (L = 3; CI = 0.33; RI = 0).**—0, present; 1, absent.

**3. Metatarsus I of males (L = 4; CI = 0.25; RI = 0.66).**—0, straight; 1, dorsoventrally curved. This character shows great variation in the degree of curvature and in the taxa in which it is present.

**4. Flexion of metatarsus I of males (L = 1; CI = 1; RI = 1).**—0, flexes outside the prolateral branch of tibial spur; 1, flexes between the two branches of tibial spur. The way that the metatarsus flexes is related to the position of the tibial spur.





Figures 3–4.—Relationship hypothesis between Ischnocolinae and other Theraphosidae groups. 3. (L = 79; CI = 0.48; RI = 0.56). Tarsal scopula coded as one character with six unordered states. 4. (L = 57; CI = 0.57; RI = 0.72). Tarsal scopula deactivated.

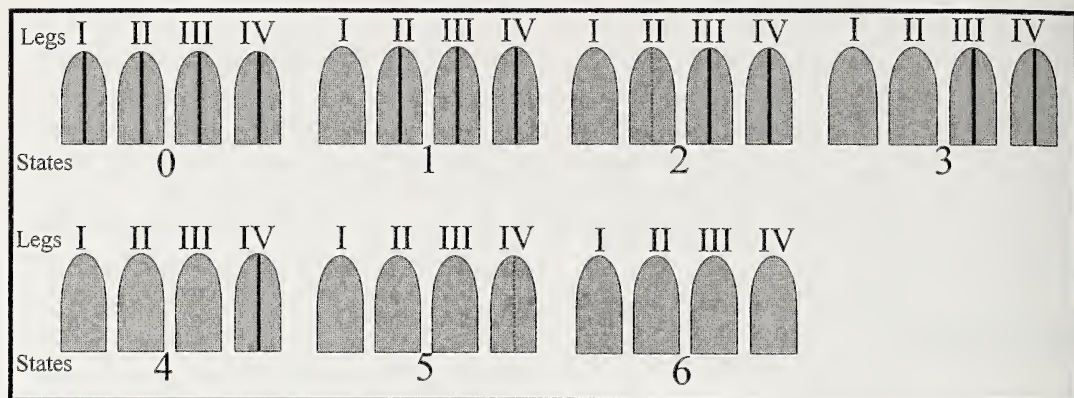


Figure 5.—Variation possibilities of Ischnocolinae tarsal scopulae. States correspond to character 30. Full line corresponds to divided scopulae with setae; dashed line corresponds to entire scopulae with band of setae.

**5. Ventral depression of the palpal tibia of males** ( $L = 1$ ;  $CI = 1$ ;  $RI = 1$ ).—0. straight or slightly curved, occupying more than half of the article; 1. sigma-like, occupying half the article. Autapomorphic for *I. algericus*. Diagnostic for the genus *Ischnocolus* (Raven 1985).

**6. Palpal bulb** ( $L = 1$ ;  $CI = 1$ ;  $RI = 1$ ).—0. apical keel absent; 1. apical keel present. The presence of keels on the bulb is a synapomorphy of Theraphosinae (Raven 1985; Perez-Miles *et al.* 1996; Bertani 2000). However, small keels were observed on the bulb of some *Oligoxystre* species. These are not considered homologous to the Theraphosinae bulb keels.

**7. Prolateral keels on the palpal bulb** ( $L = 1$ ;  $CI = 1$ ;  $RI = 1$ ).—0. absent; 1. present. Synapomorphy of Theraphosinae (Raven 1985; Perez-Miles *et al.* 1996; Bertani 2000).

**8. Subtegulum** ( $L = 1$ ;  $CI = 1$ ;  $RI = 1$ ).—0. narrow, not extending over the tegulum; 1. wide, extending over the tegulum. Synapomorphy of Theraphosinae (Raven 1985; Perez-Miles *et al.* 1996).

**9. Ventral region of the cymbium** ( $L = 3$ ;  $CI = 0.33$ ;  $RI = 0.6$ ).—0. as wide as long; 1. longer than wide. This character is very common among Ischnocolinae although it does not represent a synapomorphy for this group.

**10. Size of the lobes of cymbium** ( $L = 1$ ;  $CI = 1$ ;  $RI = 1$ ).—0. similar; 1. different.

**11. Lobular state of spermathecae** ( $L = 3$ ;  $CI = 0.33$ ;  $RI = 0.71$ ).—0. unilobular (Fig. 7); 1. multilobular (Fig. 8).

**12. Lateral lobe of spermathecae** ( $L = 2$ ;  $CI = 0.5$ ;  $RI = 0.5$ ).—0. absent (Fig. 7); 1. present (Fig. 8).

**13. Maxillae** ( $L = 2$ ;  $CI = 0.5$ ;  $RI = 0.87$ ).—0. many cuspules (more than 50); 1. few cuspules (less than 45).

**14. Labium** ( $L = 6$ ;  $CI = 0.33$ ;  $RI = 0.5$ ) **ordered**.—0. cuspules absent; 1. few cuspules (less than 10); 2. many cuspules (more than 15).

**15. Labium shape** ( $L = 5$ ;  $CI = 0.4$ ;  $RI = 0.57$ ).—0. much wider than long (2.5–3 times wider); 1. almost as wide as long (less than 2 times wider); 2. longer than wide.

**16. Tarsal claw** ( $L = 5$ ;  $CI = 0.6$ ;  $RI = 0.6$ ).—0. bare, without teeth; 1. two rows of teeth; 2. median row of teeth; 3. prolateral row of teeth; 4. single tooth.

**17. Tarsal claw with teeth** ( $L = 1$ ;  $CI = 1$ ;  $RI = 1$ ).—0. present on all legs; 1. present on anterior legs (I–II).

**18. Posterior sternal sigilla** ( $L = 3$ ;  $CI = 0.33$ ;  $RI = 0.33$ ).—0. marginal; 1. submarginal.

**19. Metatarsus I** ( $L = 1$ ;  $CI = 1$ ;  $RI = 1$ ).—0. more than  $\frac{3}{4}$  of the article scopulate; 1. less than half of the article scopulate.

**20. Metatarsus IV** ( $L = 4$ ;  $CI = 0.25$ ;  $RI = 0.62$ ).—0. less than half of the article scopulate; 1. more than half of the article scopulate.

**21. Legs spines** ( $L = 3$ ;  $CI = 0.66$ ;  $RI = 0$ ) **ordered**.—0. many spines, especially on tibia and metatarsus; 1. few reduced spines, on the apical region of tibia and metatarsus; 2. spines absent. The presence of several



spines was considered plesiomorphic for Theraphosoidina (Raven 1985). Representatives of Aviculariinae Simon 1874 show a reduced number of leg spines. Bertani (2002) demonstrated that state 2 is a synapomorphy for Aviculariinae *sensu stricto*.

**22. Tarsal scopula I (L = 2; CI = 0.5; RI = 0.85).**—0. divided by a longitudinal band of setae; 1. entire.

**23. Tarsal scopula II (L = 4; CI = 0.5; RI = 0.86) ordered.**—0. divided by a longitudinal band of setae; 1. entire with a longitudinal band of setae; 2. entire. In the present study a third state was identified which differs from state 0 in having type A setae (Rovner 1978; Pérez-Miles 1994) mixed with type B setae (Rovner 1978; Pérez-Miles 1994). In this state the tarsal scopula is not divided but there are lined setae forming a longitudinal band.

**24. Tarsal scopula III (L = 1; CI = 1; RI = 1).**—0. divided by a longitudinal band of setae; 1. entire.

**25. Tarsal scopula IV (L = 2; CI = 1; RI = 1) ordered.**—0. divided by a longitudinal band of setae; 1. entire with a longitudinal band of setae; 2. entire.

**26. Clypeus (L = 3; CI = 0.66; RI = 0.87).**—0. absent; 1. present, narrower than the diameter of the anterior median eyes; 2. present, wider than the diameter of the anterior median eyes.

**27. Urticating hair type III (L = 1; CI = 1; RI = 1).**—0. absent; 1. present. Synapomorphy of Theraphosinae (Raven 1985; Pérez-Miles et al. 1996).

**28. Apical article of posterior lateral spinnerets (L = 1; CI = 1; RI = 1).**—0. domed or rounded; 1. digitiform. This character is widely used to separate Barychelidae from Theraphosidae, the latter presenting the distal article of the PLS digitiform. However, among Barychelidae this character shows great variation making it impossible to place some representatives within either family.

**29. Anterior maxillary projection (L = 1; CI = 1; RI = 1).**—0. poorly developed; 1. developed.

**30. Tarsal scopula I-IV (L = 9; CI = 0.66; RI = 0.92) (Fig. 5).**—0. all scopula divided; 1. only tarsal scopula I entire; 2. only tarsal scopula I entire and scopula II entire with a longitudinal band of setae; 3. only tarsal scopula I and II entire; 4. tarsal scopula I-

III entire; 5. tarsal scopula I-III entire and scopula IV entire with a longitudinal band of setae; 6. all tarsal scopula entire. Although state 1 was not observed in any of the specimens examined in this study, it was included in the matrix since it was observed in an ontogenetic series. The exuvia of a specimen of *Grammostola actaeon* (Pocock 1903) was observed and it demonstrated that from state 0 to 2, two steps must be counted since the tarsal scopula II does not turn into undivided with a band of setae unless the scopula I is undivided.

## RESULTS

The first cladogram (Fig. 1) refers to the tarsal scopula character separated into four individual characters (characters 22-25). It resulted in a single tree (L = 72; CI = 0.54; RI = 0.74). It shows that part of Ischnocolinae, represented by the taxa (*Holothele rondoni*(*Sickius longibulbi*(*Ischnocolus algericus*+*Catumiri*))), is monophyletic. The remaining Ischnocolinae form a distinct group with Harpactirinae Pocock 1897, Theraphosinae and Aviculariinae. This hypothesis suggests that part of Ischnocolinae is the sister-group to the polytomy presented by Raven (1985) solving in part the cladogram presented in that study (Fig. 6).

The second cladogram (Fig. 2) refers to the tarsal scopula coded as a single character with six ordered states (character 30). It resulted in a single tree with the same topology and indices of the first cladogram but with different optimizations in the following nodes: *Catumiri petropolium*; ((Genus 1((*Tapinauchenius* sp.((*Pterinochilus murinus*(*Avicularia avicularia*(*Euathlus vulpinus*+*Vitalius vellutinus*)(*Oligoxystre* spp.)))); ((*Tapinauchenius* sp.((*Pterinochilus murinus*(*Avicularia avicularia*(*Euathlus vulpinus*+*Vitalius vellutinus*)(*Oligoxystre* spp.)))); (*Pterinochilus murinus*(*Avicularia avicularia*(*Euathlus vulpinus*+*Vitalius vellutinus*)(*Oligoxystre* spp.)) and ((*Pterinochilus murinus*(*Avicularia avicularia*(*Euathlus vulpinus*+*Vitalius vellutinus*)). Moreover it showed no homoplasies for the tarsal scopula character.

The third cladogram (Fig. 3), which is a consensus of 16 trees, refers to the tarsal scopula coded as a single character with six independent states. The only monophyletic groups in this tree are (*Euathlus vulpi-*

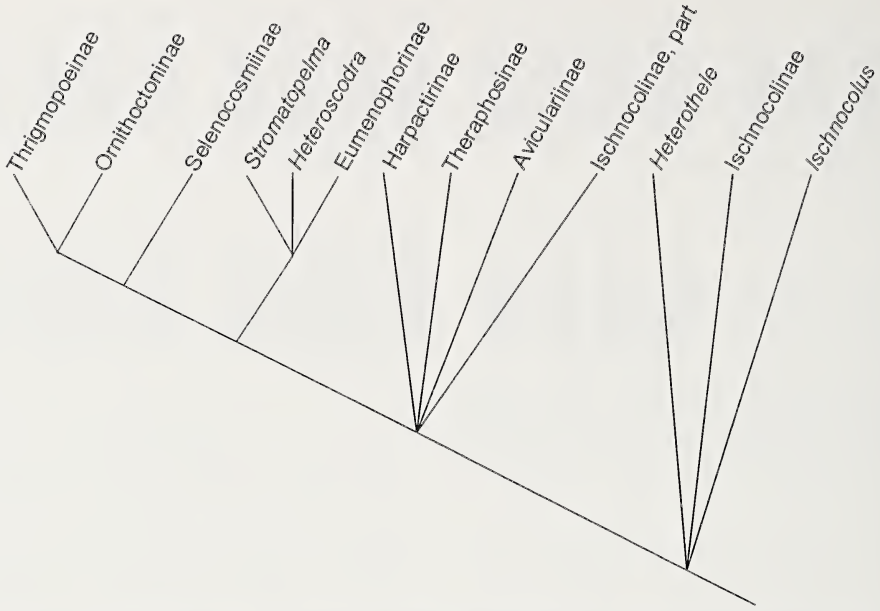


Figure 6.—Relationship hypothesis among Theraphosidae subfamilies (Raven 1985).

*nus*+*Vitalius vellutinus*); (*Tapinauchenius* sp.+*Avicularia avicularia*); *Catumiri* spp. and *Oligoxystre* spp.

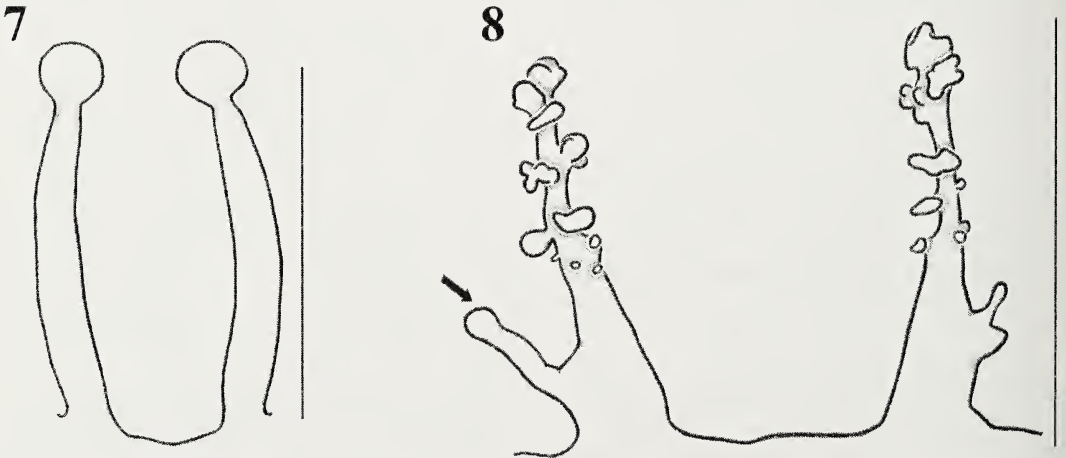
The fourth cladogram (Fig. 4), which is a consensus of two trees, refers to the tarsal scopula character deactivated in the matrix. The only Ischnocolinae representatives that formed a monophyletic group are (*Oligoxystre* spp.+*Ischnocolus algericus*).

The tarsal scopula I condition did not show any relation to spider size ( $t = -0.80433$ ;  $P = 0.438247$ ) (graphic 1). Divided tarsal scopula

I is present in large species (*H. rondoni*) and entire scopula I in small (Genus 2 spp.).

#### DISCUSSION

**Anterior-posterior gradation.**—Some characters (e.g. number of spines, development of teeth on the paired tarsal claws) show an anterior-posterior gradation that was described by Raven (1985). Concerning the tarsal scopula, many species of Ischnocolinae present different states on legs I–IV, where there is a tendency towards the anterior legs



Figures 7–8.—7. Unilobular spermathecae (*Catumiri argentinense*). 8. Multilobular spermathecae, arrow showing the lateral lobe (*Oligoxystre* sp4).



presenting the apomorphic state. If the plesiomorphic state (divided scopula) is present on leg I, then legs II–IV always show the same state. If the apomorphic state (entire scopula) is present on leg I, legs II–IV may or may not have the scopulae entire. The opposite happens if we observe the state of the tarsal scopula on leg IV: if scopula IV is divided, it can be entire or divided on the anterior legs. If scopula IV is entire, all the anterior legs will present the apomorphic entire state. Moreover, if all the tarsal scopulae are divided on all legs, then leg IV will present the widest band of setae dividing the scopula.

**Character dependency.**—Considering the ontogenetic differentiation (Gerschman de Pikelin & Schiapelli 1973), the anterior-posterior gradation (Raven 1985) and the variability of states (described above) of the tarsal scopula in the Theraphosidae it is reasonable to conclude that there is a dependency of this character between the legs. As such, a posterior tarsal scopula will not become entire unless the anterior one is entire during the ontogenesis and an anterior tarsal scopula will not be divided if the posterior one is entire. An ontogenetic series composed of the exuviae of a specimen of *G. actaeon* showing this sequenced transformation and all the combinations found within the Ischnocolinae (Fig. 5) confirms this character dependency.

**Tarsal scopula as a character.**—Pérez-Miles (1992) used the tarsal scopula as a character on a preliminary cladistic analysis for Theraphosinae. In this analysis the plesiomorphic state was “at least one of the tarsal scopula divided”. It means that if a certain species has the tarsal scopula IV divided, it would be coded as plesiomorphic and the state of scopula I would be ignored. It would be interesting to study the condition of the anterior tarsal scopulae in the species that have the scopula IV divided.

The use of the tarsal scopula in phylogenetics was discussed by Pérez-Miles (1994). According to him, results presented in that paper questioned the use of this character in cladistic analysis since a close relation between body size and scopula condition (small sized species tend to possess divided scopula), in Theraphosinae and Harpactirinae adults, could suggest a functional adaptation or a developmental effect. However it is admitted that the

role of this character in theraphosid evolution remains obscure. Pérez-Miles (1994) explained that the scopula of tarsus IV was the only one used in order to avoid ambiguity, since scopula division width increases on the hind legs (Raven 1985). It can be supposed that the tarsal scopula condition within Theraphosinae is either all legs with scopula divided or entire. Species of the genera *Hapalopus* Ausserer 1875 and *Homoeomma* Ausserer 1871 have all tarsal scopula divided (pers. obs.).

Ischnocolinae is a very problematic group that lacks synapomorphies (Raven 1985) and its genera and species are mostly recognized by sexual characters (e.g. spermatheca and bulb morphology; presence, absence and morphology of structures of the tibial apophysis). So far, Ischnocolinae is considered a paraphyletic subfamily and the results presented in this paper show that at least part of this group is supported by having more than half of the metatarsus IV occupied by scopula. The main difficulty to infer phylogenetic hypotheses for Ischnocolinae is the reduced number of characters that can be defined, since these spiders have a very homogeneous morphology. Different from Theraphosinae, Ischnocolinae shows a great diversity of tarsal scopula states. If the divided scopula is related to small sized species, the large ones would be more likely to present the scopula I entire, which does not happen in Ischnocolinae (Fig. 9). Since the tarsal scopula condition is not related to spider size in Ischnocolinae ( $t = -0.80433$ ;  $P = 0.438247$ ), this character might have an important role in ischnocoline phylogenetics. This importance is evident when cladogram 4 is analyzed: monophyletic groups like (*S. longibulbi*+*Pterinochilus murinus*) are based on characters that are very variable (clypeus and curvature of metatarsus I of males); the monophyletic group ((*E. vulpinus*+*V. vellutinus*)(*R. annae*(*Tapinauchenius* sp.+*A. avicularia*)) has *R. annae* (Trichopelmatinae) as the sister-group of Aviculariinae. This does not agree with the basal position of Trichopelmatinae within Theraphosidae proposed by Raven (1994). Furthermore, the position of *R. annae* within this group does not agree with the monophyly of Theraphosinae + Aviculariinae proposed by Lucas (et al. 1991) and Pérez-Miles (1992).

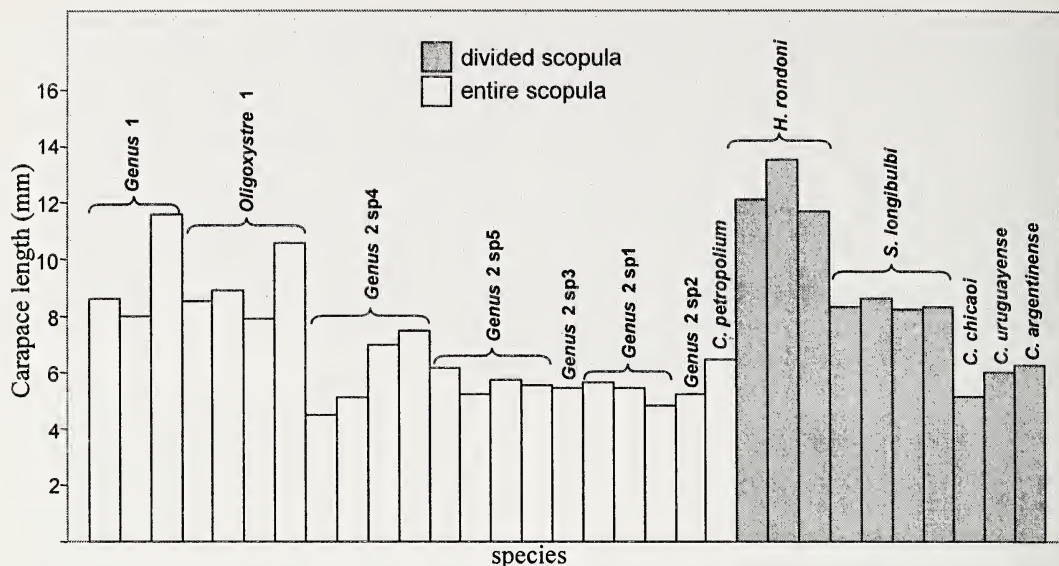


Figure 9.—Carapace length and tarsal scopula I condition for some Ischnocolinae species.

It was possible to show all the variability of the tarsal scopula condition with the six state character. There was no mask on the variation of a character using the synthetic code, contrary to Pogue & Mickevich (1990). The difference between cladograms 1 and 2 is that the second one provided no homoplasies for the tarsal scopula character. Another difference between the two optimizations is that the first cladogram has more synapomorphies on the nodes mentioned above. Since the character dependency is admitted, these synapomorphies (characters 22, 23, 24) might be false. The use of the tarsal scopula condition as six unordered states of only one character admits that the transformation from divided to entire scopula is independent in all pairs of legs. If this is true, we could find a spider with divided anterior scopula and entire posterior scopula, or even scopula I and II entire, scopula III divided and scopula IV entire. The dependency of tarsal scopula condition between the legs means that the more entire the scopula the more apomorphic conditions (states) it will show. From these results it is possible to conclude that since there is relation between tarsal scopula condition and spider size, this character should be used in cladistic analysis. Additional Ischnocolinae taxa must be included in this analysis in order to provide a better knowledge of this character.

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## A PRELIMINARY STUDY OF THE RELATIONSHIPS OF TAXA INCLUDED IN THE TRIBE POLTYINI (ARANEAE, ARANEIDAE)

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**ABSTRACT.** *Pollys* and the genera *Cyphalonotus*, *Homalopollys*, *Ideocaira*, *Kaira*, *Micropollys* and *Pycnacantha* have historically been considered members of the tribe Poltyini. There is little published information on most members of the group and their potential relationships in the context of recent advances in araneid systematics. Information is sought on possible relatives of *Pollys*. All araneid members of the group except *Pycnacantha* were added to the data matrix compiled by Scharff & Coddington (1997), which already contained *Kaira*. *Homalopollys* was found to be a tetragnathid when males were identified and was not considered further. The full data matrix of 74 taxa and 82 characters was run in PAUP\* and NONA. The resulting placement of *Pollys* was not well supported but it frequently occurred in association with members of a slightly modified version of the ‘*Hypsosinga* clade’ of Scharff & Coddington, including *Kaira*. *Cyphalonotus* may be placed close to *Araneus* and *Ideocaira* may also belong in the same area of the araneines. *Micropollys* may belong in the sister clade to these two.

**Keywords:** *Pollys*, *Cyphalonotus*, *Ideocaira*, *Micropollys*, phylogenetic relationships.

Spiders of the genus *Pollys* C.L. Koch 1843 are distributed throughout the Old World, mostly in tropical and subtropical regions. The Australasian species mimic galls or dead twigs by day and exhibit morphological modifications to enhance their cryptic disguise, making them rather odd-looking spiders. After some initial uncertainty over the affinities of the genus (Koch thought it might belong with taxa that are now included within Uloboridae) Simon (1895) placed *Pollys* in the subfamily Argiopinae as the nominative member of the tribe Poltyeae (here referred to as the Poltyini to conform with the International Code of Zoological Nomenclature). Also included by Simon were the genera *Cyphalonotus* Simon 1895, *Homalopollys* Simon 1895, *Kaira* Cambridge 1889 and *Pycnacantha* Blackwall 1865. The genera *Ideocaira* Simon 1903 and *Micropollys* Kulczyński 1911 were described later, and their authors suggested that they might be related to *Kaira* and *Pollys*, respectively. More recently they were listed as part of the Poltyini (as ‘Poltyeae’) by Dippenaar-Schoeman & Leroy (1996). Archer (1951) recognized that the male pedipalp of *Cyphalonotus* was far more complex than that of *Pol-*

*tys* and proposed a new tribe, the *Cyphalonotini*, for the former, later he decided it belonged in the ‘*Dolophini*’ (Archer 1965). None of these tribes are currently in regular taxonomic use, and I am using the Poltyini grouping in the broadest sense, including all the above genera as the basis for this study.

The phylogenetic analysis of araneid taxa by Scharff & Coddington (1997) was based on taxa selected from Simon’s tribes (or the earlier subfamily versions thereof), and *Kaira* was used as the representative of the Poltyini. The results suggested that *Kaira* should be placed in the ‘*Hypsosinga* clade’ in the mid-basal araneines. If Simon was correct in his affiliations of taxa this is where *Pollys*, and the remaining Poltyini taxa, should also belong. However, Scharff & Coddington (1997) also found that some of Simon’s taxa were seriously polyphyletic. As Archer may have realized during his work on *Cyphalonotus*, the possibility of errors in Simon’s grouping of the Poltyini was compounded by his lack of knowledge of the males of almost all the genera in the tribe. Simon’s assemblage was apparently based on the irregular form of the abdomen, slightly unusual eye arrangements



and the strong macrosetae on the legs of the three genera which are now known to prey mainly on moths (*Kaira*, *Pollys* and *Pycnacantha*) (Stowe 1986; Dippenaar-Schoeman & Leroy 1996). There is a confusing mixture of similarities and contradictions amongst characters within the genera of this putative group and also with respect to genera elsewhere in the Araneidae. These conflicts make the assessment of the likely placement of *Pollys* within the Araneidae problematic.

The primary motivation for this work was to attempt to establish some possible relatives of *Pollys* which could provide a sensible out-group taxon for an analysis of the Australasian *Pollys* taxa. Most of the other putative Poltyini would not be suitable for this, even if they were closely related, because of the problems of obtaining suitable recent material for destructive techniques such as the extraction of DNA. Nevertheless, I was still intrigued by some of the characters exhibited by these taxa and their superficial similarities to *Pollys*. Therefore, there were two goals to this study. The first aim was to test whether *Pollys* might indeed belong in the '*Hypsosinga* clade' of Scharff & Coddington 1997 (and if not, where). Secondly, to find out whether, without any changes or additions to the characters used, the Poltyini would emerge as a monophyletic grouping within the context of the taxa examined by Scharff & Coddington 1997.

## METHODS

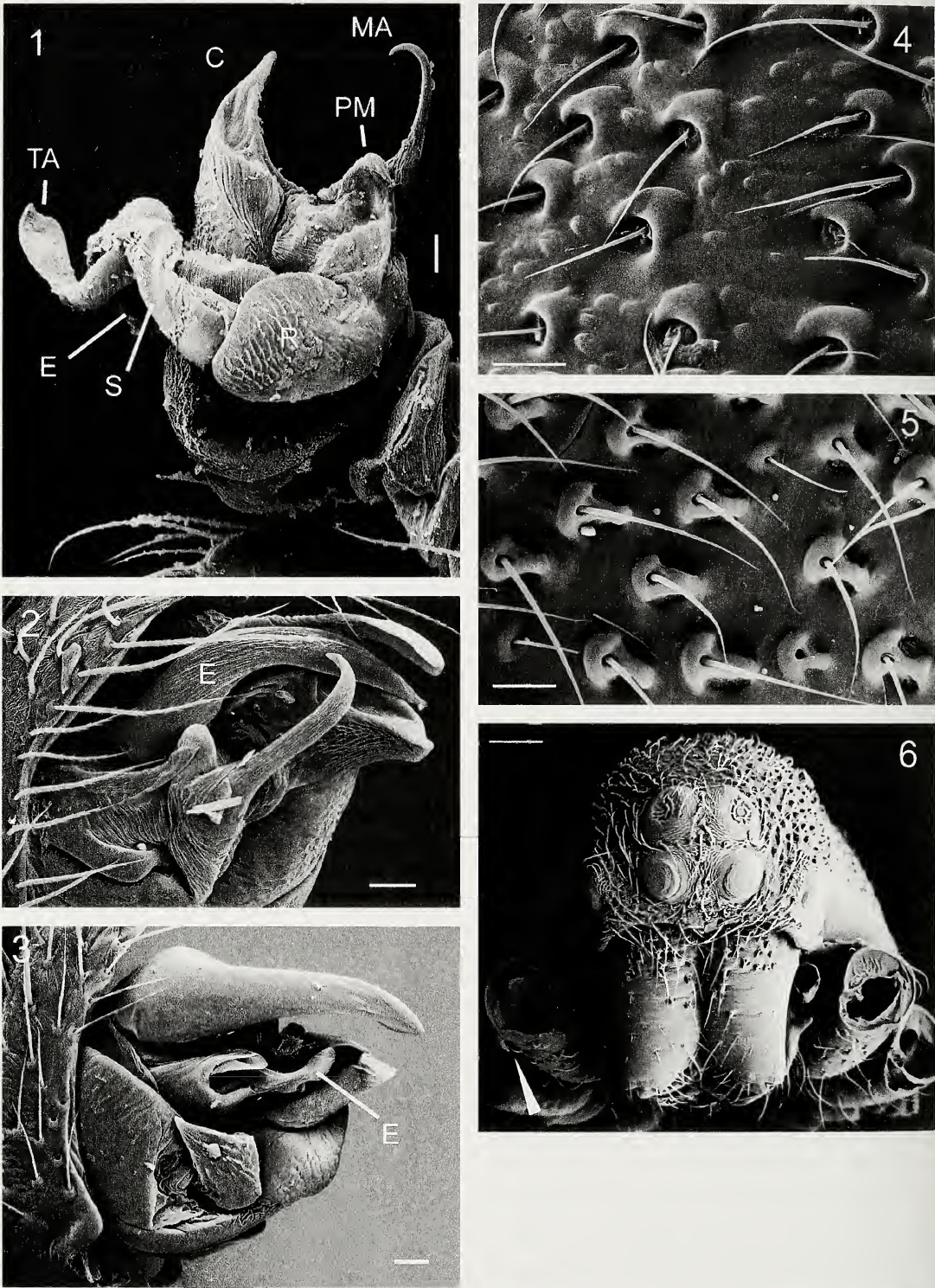
**Taxa.**—The genus *Pycnacantha* was excluded, as no male specimens were available. *Kaira* was recently revised by Levi (1993) and was included by Scharff & Coddington 1997 in their study. The other genera of Poltyini are generally poorly known and it was first necessary to identify males for *Homalopollys*, *Ideocaira* and *Micropollys*, which are described only from females. When *Homalopollys* males were found it became apparent that this taxon is in fact a tetragnathid. This genus was therefore excluded from further analysis here. The female type of *Ideocaira transversa* Simon 1903 has been examined, and unpublished drawings of the female type of *Micropollys placenta* Kulczyński 1911 were supplied by H. Levi. Unfortunately, none of the species in which males could be matched to females represented the type species of the ge-

nus. For *Cyphalonotus*, the expanded pedipalp is from a different species to that used for scoring general characters (necessitated by the need to use material from the only vial which contained more than a single male). The structures visible on the unexpanded pedipalp of the species against which other male and female characters were scored appear to be similar; there are also no scoreable differences in the general attributes in the males of both species. Neither species has been identified, the type species, *C. larvatus* (Simon 1881), is recorded from Congo and East Africa (Platnick 2005). This leaves *Pollys illepidus* C.L. Koch 1843 as the only type species used in this analysis. Although this is far from ideal, the nature of this data set, with a rather high proportion of taxa to characters, meant robust results were unlikely even before adding additional taxa (Scharff & Coddington 1997). Therefore, I did not expect to achieve precise results in this tentative exploration of these genera and any more rigorous analysis would need to address these issues.

**Abbreviations.**—The following abbreviations for morphological features were used throughout the text and figures: C = conductor; CY = cymbium; E = embolus; MA = median apophysis; PC = paracymbium; PM = paramedian apophysis; R = radix; S = stipes; SEM = scanning electron microscope; T = tegulum; TA = terminal apophysis; TL = tegular lobe. The following abbreviations were used for repository institutions: AM = Australian Museum, Sydney, Australia; MNHNP = Muséum National d'Histoire Naturelle, Paris, France; MRAC = Koninklijk Museum voor Midden Afrika, Tervuren, Belgium; NCAP = National Collection of Arachnida, Pretoria, South Africa; NHRM = Swedish Museum of Natural History, Stockholm, Sweden; QM = Queensland Museum, Brisbane, Australia; RMNH = National Museum of Natural History, Leiden, The Netherlands; UNAM = Instituto de Biología, Universidad Nacional Autónoma de México, Mexico D.F., Mexico; ZMB = Museum für Naturkunde, Zentralinstitut der Humboldt-Universität, Berlin, Germany.

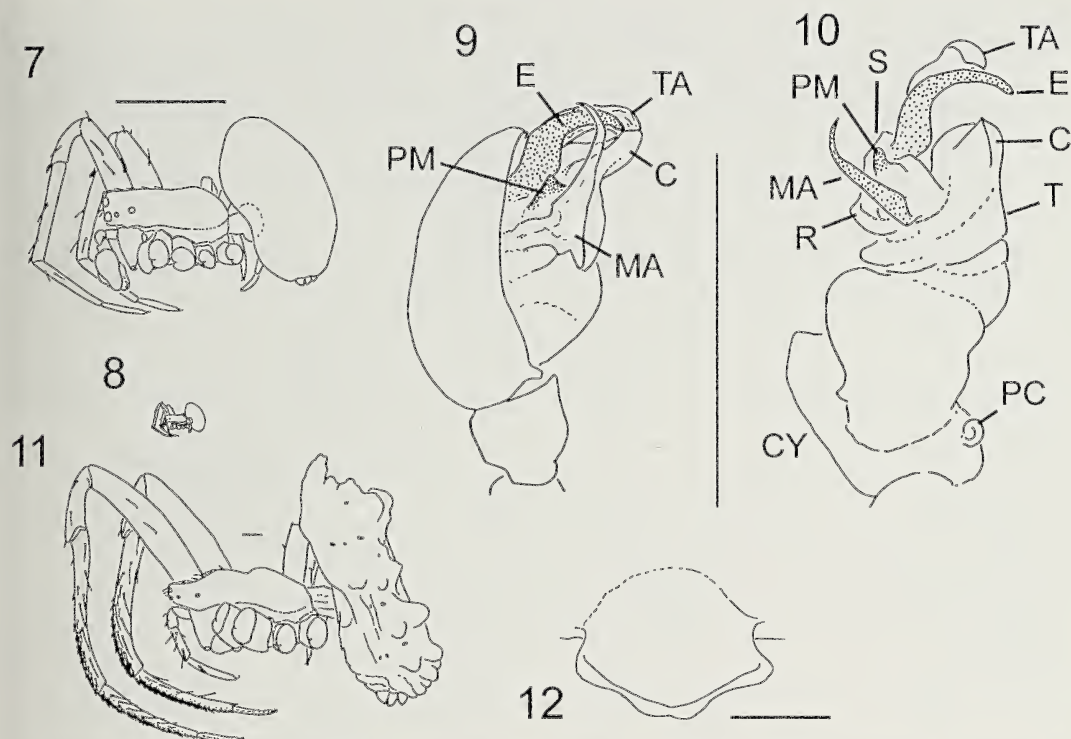
**Characters.**—The character attributes for each of the selected taxa were examined and scored according to the methods of Scharff & Coddington 1997. The specimens examined are shown in Table 1 and attribute codings are





Figures 1–6.—Scanning electron micrographs of *Poltys* and *Micropoltys*: 1. *Poltys illepidus* from Trinity Park, male; expanded pedipalp, apico-dorsal view; 2. *Poltys illepidus* from Lakeland, male, pedipalp, prolateral. 3–6. *Micropoltys* sp. from W of Cape Kimberley, male: 3. Pedipalp, prolateral; 4, 5. Modified setal bases and sensory seta on carapace and sternum, respectively; 6. Prosoma, frontal view. See text for abbreviations. Scale bars Figs. 1, 2 (30 μm), Figs. 3–5 (20 μm), Fig. 6 (100 μm).





Figures 7-12.—*Poltys illepidus*: 7-9. Male from Trinity Park: 7. General lateral view; 8. Ditto but at same scale as female; 9. Left pedipalp, prolateral. 10. Male from Rockhampton, left pedipalp, expanded, prolateral. 11. Female from Trinity Park: General lateral view. 12. Female from Brisbane, epigynum, ventral. See text for abbreviations. Scale bars Figs. 7, 11 (1 mm), Figs. 9-10, 12 (0.5 mm).

shown in Table 2. The full list of characters is not repeated here but most characters are adequately illustrated in Figs. 1-30. Some characters, listed below, do require some comment on their interpretation in relation to the Scharff & Coddington 1997 analysis.

Character 11 and 12: Median apophysis of male pedipalp with bifid prong or threadlike spur. The apically directed hook-like portion of the *Poltys* MA is very distinctive (Figs. 1, 9). However, it does not conform totally to either of the diagnoses for these character states.

Character 19: Stipes absent or present. In *Micropoltys* the sperm duct appears to pass from the radix, through the base of the distal haematodocha and straight into the embolus. There is apparently no sclerite as such between the two, so this is scored absent [0] (Fig. 28).

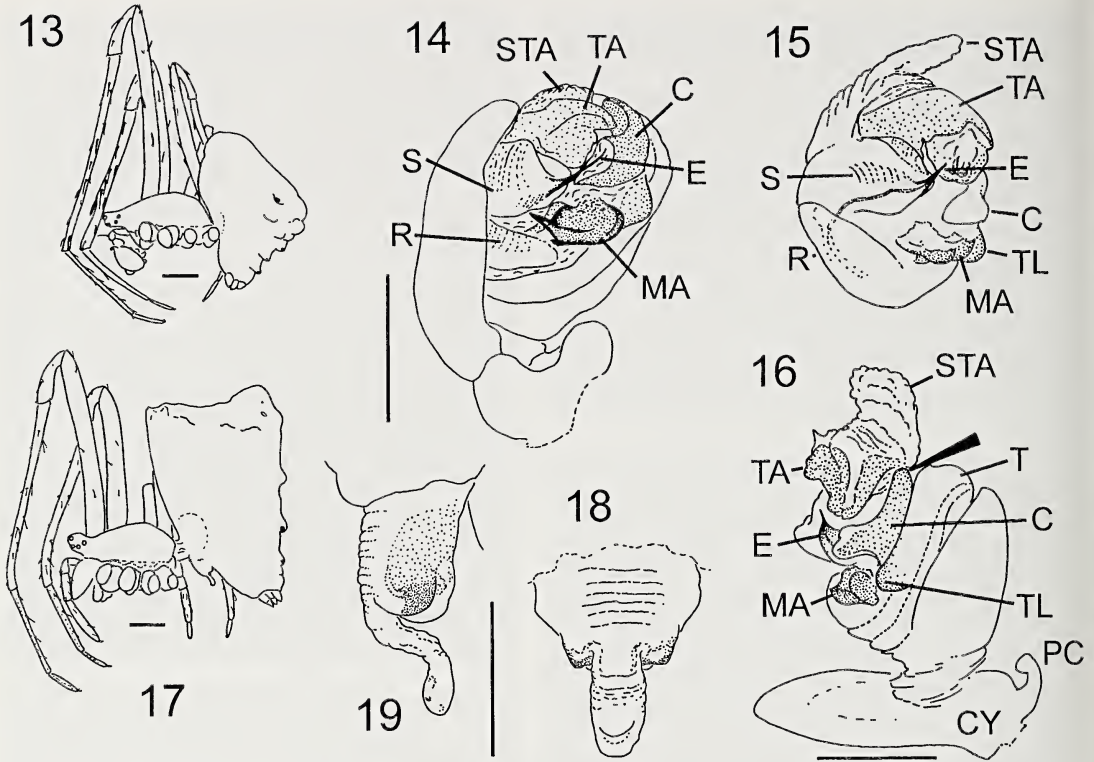
Character 23: Tip of male pedipalp embolus simple or with cap. Only *Poltys* and *Micropoltys* pedipalps have been examined under SEM (Figs. 2, 3). There is no indication on

either of these that any part is designed to break off, or has already done so. These are scored as simple [0]. The attributes of the other genera are unknown so they are scored [?].

Character 30: Scape with pocket near tip, absent or present. *Poltys illepidus* have a broad turned-over rim along the whole of the posterior margin of the epigyne (Fig. 12). I have interpreted this as a (rather wide) pocket present [1]. *Micropoltys* females have at least a sharp depression which is tentatively also scored here as a pocket present [1] (Fig. 30).

Characters 33 and 34: Coxa I hook and femur II groove. Among these taxa, all of the males with similarly sized females have these features (e.g. coxal hook arrowed in Fig. 6, *Micropoltys*).

Character 46: Clypeal tooth of females absent or present. Both males and females of the *Micropoltys* species figured have a rather rounded clypeal tooth. The male is shown in Fig. 6, but the tooth is more developed in females. This character is not present in Levi's



Figures 13–19.—*Cyphalonotus* sp.: 13, 14. Male from Natal: 13. General lateral view; 14. Left pedipalp, prolateral; 15, 16. Male from Misahöhe: Left pedipalp expanded, prolateral and retrolateral (different species to Fig. 14). 17–19. *Cyphalonotus* sp. from Natal, female: 17. General lateral view; 18, 19. Epigynum, ventral and lateral. See text for abbreviations. Scale bars Figs. 13, 17 (1 mm), Figs. 14–16, 18, 19 (0.5 mm).

drawing of the type female of *Micropoltys placenta* but I have scored it as present [1].

Character 50: Ratio of lateral eye–median eye separation,  $< 1$  or  $> 1$ . *Poltys* and *Micropoltys* are unusual among araneids in that they have widely separated lateral eyes, so there is no lateral eye group as such (Figs. 7, 11, 26, 29). In applying this character to these genera I took the Scharff & Coddington 1997 instructions literally, and used the distance at the widest point, i.e. that to the posterior eye, so that the separation is scored as  $> 1$  [1].

Characters 59 and 60: Abdominal shape. Both male and female *Ideocaira triqueta* Simon 1903 have strongly triangular abdomens, which are widest anteriorly (Fig. 24, female). The females of *I. triqueta* vary in their relative dimensions, some being wider than long and some the reverse. However, the female of *I. transversa*, the type species, is distinctly wider, so I have used this to decide the matter and scored Character 60 as wider [1].

Character 67: Tactile setal bases on carapace and abdomen, normal or gasteracanthine-shaped. *Micropoltys* has rather distinctive setal bases over much of the prosoma, including the basal chelicerae (Fig. 6). There are none on the dorsum of the abdomen, but they do occur around the pedicel on the venter. Some of these bases and the setae themselves (Fig. 4) are extremely similar to those figured by Scharff & Coddington 1997 and I have scored them as gasteracanthine-like [1]. Those on the sternum (Fig. 5) and around the eye region and chelicerae are further modified, with an anteriad-projecting lamella and deep pits on each side.

Characters 74 and 75: Orb web and sticky spiral. Joseph Koh has provided me with a photograph of *Cyphalonotus* in an orb web. I cannot see anything to suggest that it is not a normal araneid web and so have scored Character 75, sticky spiral, as present [0]. (This

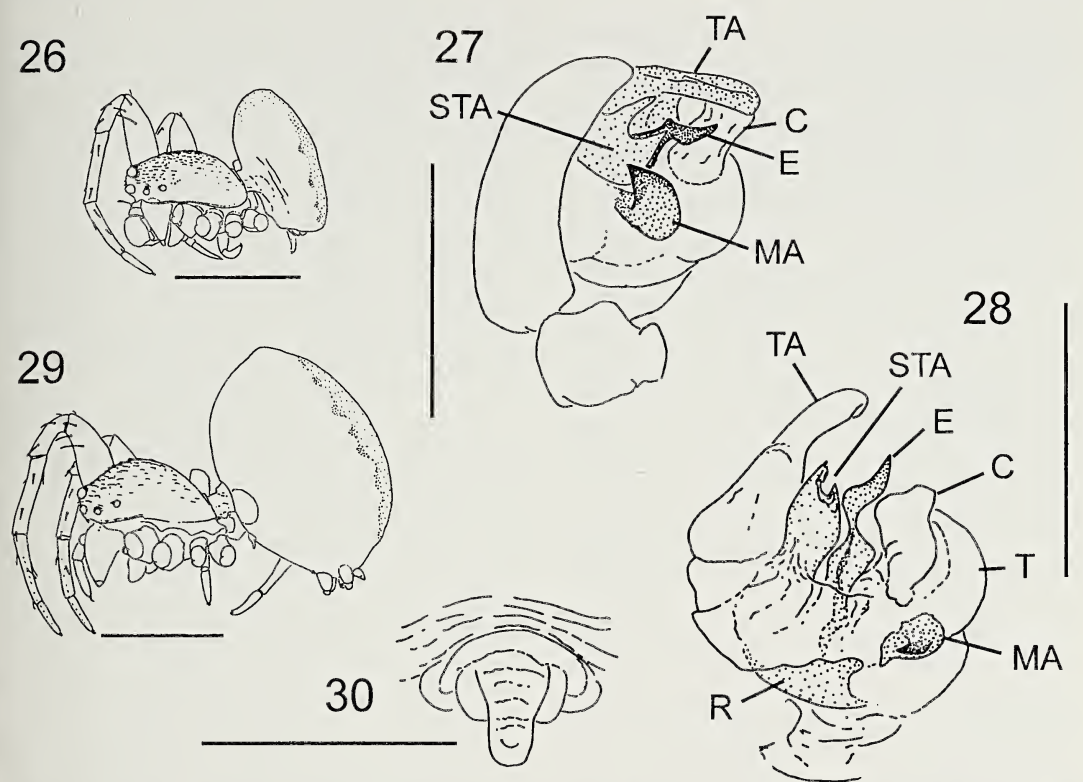


Table 1.—Details of specimens examined in this study.

Sex & Species	Locality data	Coordinates	Repository & No.	Used for
♂ ♀ <i>Cyphalonotus</i> sp.	Natal, South Africa		MNHNP 19654	All codings; Figs. 13, 14, 17–19
♂ <i>Cyphalonotus</i> sp.	Misahöhe, Togo	06°57'N, 00°35'E	ZMB (unreg'd)	Expanded pedipalp; Figs. 15, 16
♂ ♀ <i>Ideocaira triqueta</i>	Mzimhlava river mouth, Lusikisiki district, Eastern Cape, South Africa	31°22'S, 29°35'E	MRAC 166621	All codings; Figs. 20–25
♀ <i>Ideocaira triqueta</i>	Port Elizabeth, Eastern Cape, South Africa	33°58'S, 25°35'E	MNHNP 18508	Types (2), used to confirm ID
♀ <i>Ideocaira transversa</i>	Natal, South Africa		MNHNP 16334	Type
♂ <i>Micropoltys</i> sp.	Cape Kimberley, Queensland, Australia	16°16'S, 145°28'E	AM KS86251	Pedipalp; Fig. 27
♂ <i>Micropoltys</i> sp.	Cape Kimberley, Queensland, Australia	16°16'S, 145°28'E	AM KS86252	Expanded pedipalp, general codings; Figs. 26, 28
♂ <i>Micropoltys</i> sp.	W of Cape Kimberley, Queensland, Australia	16°15'S, 145°26'E	AM KS86740	SEM; Figs. 3–6
♀ <i>Micropoltys</i> sp.	Cooktown, Queensland, Australia	15°29'S, 145°15'E	AM KS57876	General codings; Fig. 29
♀ <i>Micropoltys</i> sp.	W of Cape Kimberley, Queensland, Australia	16°15'S, 145°26'E	AM KS57890	Epigynum; Fig. 30
♂ <i>Poltys illepidus</i>	Trinity Park, N Cairns, Queensland, Australia	16°48'S, 145°42'E	AM KS86253	General codings; Figs. 7–9
♂ <i>Poltys illepidus</i>	Rockhampton, Queensland, Australia	23°22'S, 150°29'E	AM KS58033	Expanded pedipalp; Fig. 10
♂ <i>Poltys illepidus</i>	Trinity Park, N Cairns, Queensland, Australia	16°48'S, 145°42'E	AM ex eggsac laid by KS86257	SEM; Fig. 1
♂ <i>Poltys illepidus</i>	Lakeland, SW of Cooktown, Queensland, Australia	15°50'S, 144°53'E	AM KS58017	SEM; Fig. 2
♀ <i>Poltys illepidus</i>	Trinity Park, N Cairns, Queensland, Australia	16°48'S, 145°42'E	AM KS86258	General codings; Fig. 11
♀ <i>Poltys illepidus</i>	Brisbane, Queensland, Australia	27°30'S, 152°58'E	QM S20786	Epigynum; Fig. 12
♀ <i>Poltys illepidus</i>	Edmonton, Queensland, Australia	17°01'S, 145°44'E	AM KS86310	SEM (spinnerets, not figured)







Figures 26–30.—*Micropoltyys* sp.: 26–28. Male from Cape Kimberley: 26. General lateral view; 27, 28. Left pedipalp, prolateral and expanded, apico-dorsal view. 29. Female from Cooktown, General lateral view; 30. Female from W of Cape Kimberley, Epigynum, ventral. See text for abbreviations. Scale bars Figs. 26, 29 (1 mm), Figs. 27, 28, 30 (0.25 mm).

hsearch start=current nchuck=0 chuck-  
score=0;

The first line keeps only 5 trees from each island sampled, preventing the tree buffers from filling with thousands of trees and increasing the chances of finding all islands of trees. One thousand replicates are carried out, each time with the taxa added in a random order. The default branch swapping algorithm TBR (tree bisection reconnection) is used. The

order of the resulting trees is randomized before entering the second line of command. The second line swaps on the trees kept from the first search to completion.

All data was also run in NONA (Goloboff 1993) using the standard commands, as recommended by Miller (2000):

mult\*1000;  
max\*; or jump\*1;

Before using any consensus method in

Table 2.—Extended.

Character number				
4	5	5	6	6
1234567890	1234567890	1234567890	1234567890	1234567890
0000100010	110000-000	0001000100	2??11?????	??
0000100011	110000-061	0001000100	21????????	??
0000110001	110000-000	00000011??	??????????	??
0000000011	110000-000	1001000100	2101000200	00

PAUP\* it is desirable to check through the topologies and delete any with zero-length branches (Scharff & Coddington 1997). NONA's algorithms are better in this regard but the program can still produce uncollapsed polytomies which are suboptimal once collapsed. Scharff & Coddington 1997 also advocate the filtering of tree sets to remove those trees containing polytomies for which there is a more resolved solution present. With the solution present in another, otherwise identical tree, it is reasonable to support their interpretation as 'soft' polytomies, i.e. irresolution due to a lack of data, rather than 'hard' polytomies which is an assertion of simultaneous cladogenesis (Coddington & Scharff 1996). The tree data set can be filtered in PAUP\* but the removal of trees containing zero-length branches is more problematic. Two methods used here are the manual removal of the topologies with assigned zero-length branches from a saved PAUP\* tree file, or alternatively using WinClada (Nixon 1999–2002) by a process of collapsing unsupported nodes then removing suboptimal trees. The tree set produced by NONA can also be 'cleaned up' using WinClada, but cannot easily be filtered. While tree data sets from either PAUP\* or NONA can be imported into WinClada and back into NONA, once exported from PAUP\* retrieving them is difficult. An Adams consensus (Adams 1972; implemented in PAUP\*) was required to examine whether clades might be recovered which would otherwise not be found by more simple consensus methods. Consequently, the tree set primarily used is that produced by PAUP\*'s filtering and the manual removal of topologies with zero-length branches. However, this is not the same as the set obtained by passing the filtered trees through the WinClada routine. It was decided that both methodologies should be used to confirm that any conclusions drawn were supported in both cases. Strict, majority-rule and Adams consensus trees were produced in PAUP\* and all topologies were examined using WinClada.

## RESULTS

PAUP\* initially found 948 minimal length trees (300 steps). This was reduced to 376 trees by filtering and finally 156 trees after manual removal of topologies with zero length internal branches (referred to subse-

quently as the 'manual tree set'). After passing the filtered set through WinClada, 132 topologies remained (the 'WinClada tree set'). NONA found 344 initial trees using the jump\*1 command (length 300, as PAUP\*), which is reduced to 232 trees after collapsing polytomies in WinClada. These topologies are the same as those in the PAUP\* data set (shown by putting the unfiltered PAUP\* tree set through WinClada: the same 232 trees are found). Using the max\* swapping algorithm was less effective and only recovered 308 trees, or 192 trees post WinClada.

All the consensus trees maintain the out-group structure and basal araneid placement of *Chorizopes* O.P.-Cambridge 1870 found by Scharff & Coddington 1997 (fig. 82, Fig. 31). The araneines become a bush beyond this point in the strict consensus tree (Fig. 31), although with a few resolved terminal clades. All the Poltyini examined here are found within the Araneinae (*sensu* Scharff & Coddington 1997 except for *Scoloderus* Simon 1887). The majority-rule tree produced from the WinClada tree set is slightly less resolved than that shown from the manual tree set (Fig. 32): two additional levels are collapsed in the araneines, so that *Hypsosinga* Ausserer 1871 and *Dolophones* Walckenaer 1837 are in the main araneine 'bush'.

The position of *Polty*s within the araneines is unresolved by all the consensus methods (Figs. 31–33). The character partition table from PAUP\* indicates that *Polty*s pairs with *Zygiella* F.O.P.-Cambridge 1902 (31% of trees) or *Kaira* (15%) in the manual tree set, and there are several combinations of a clade involving *Polty*s and some or all of *Zygiella*, *Kaira*, *Metepeira* F.O.P.-Cambridge 1903, *Singa* C.L. Koch 1836, and *Larinia* Simon 1874. Examining trees, these sub-arrangements add up to 61% of topologies. This group is all of the Scharff & Coddington 1997 'Hypsosinga clade' (clade 44), except *Hypsosinga* itself and with the addition of *Larinia*, which also frequently came into this clade in the Scharff & Coddington 1997 analysis. In other topologies there is usually a series of single taxon 'steps' in the basal araneines, in which *Polty*s occurs, often with other parts of the 'Hypsosinga clade' emerging as adjacent steps. In many trees with this type of topology, *Witica* O.P.-Cambridge 1895 and *Arachnura* Vinson 1863 are also present in the very base of the



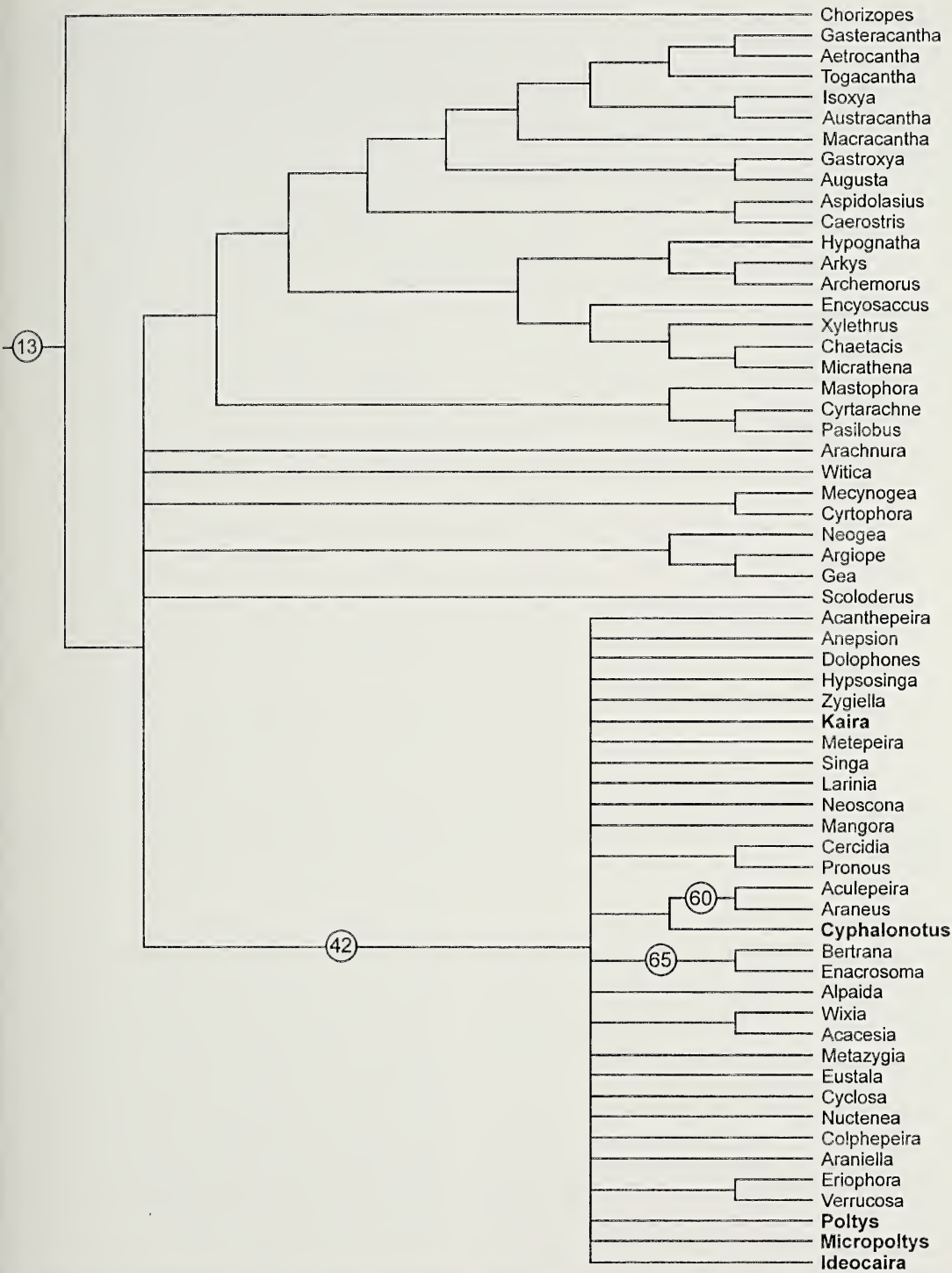


Figure 31.—Strict consensus of the Araneidae for the data of Scharff & Coddington 1997 and taxa from the Poltyini (in bold). Clade numbers show relevant areas of agreement with Scharff & Coddington 1997 (fig. 82).





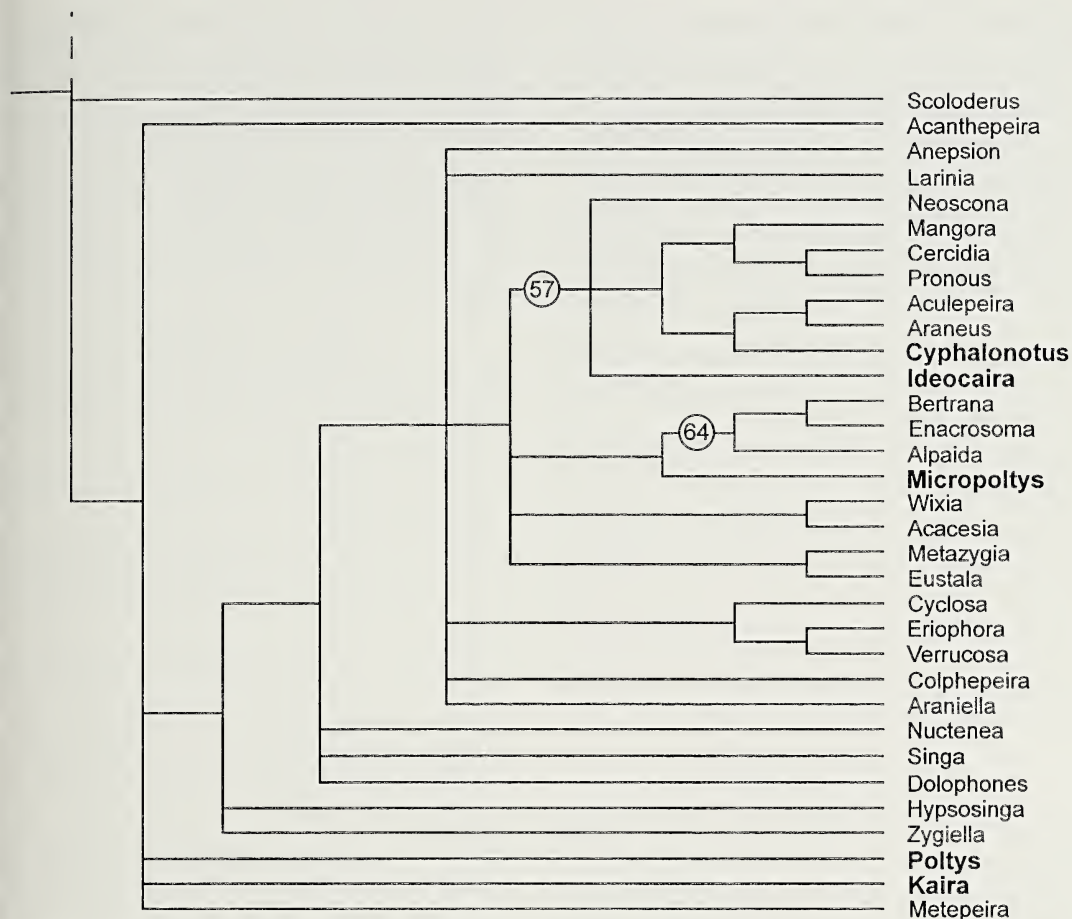


Figure 33.—Adams consensus of the Araneinae for the data of Scharff & Coddington (1997) and taxa from the Poltyini (in bold). Clade numbers show relevant clades analogous to those found by Scharff & Coddington 1997.

serve to suggest the taxa among which these new additions might be placed.

The question of whether *Poltys* should be included in the '*Hypsosinga* clade' remains uncertain. In these results it is most frequently associated with one or more of the genera *Zygiella*, *Kaira*, *Metepeira*, *Singa* and *Larinia*, most of which are indeed from this clade. However, the inclusion of *P. illepidus* in the data set destabilises the arrangement found by Scharff & Coddington 1997 and reduces the former clade to a loose association of genera with variable placement within the Araneinae. Despite this, one of these genera would provide the best choice of outgroup given the current evidence. However, a cautionary comment about other *Poltys* taxa is required. One of the criteria Scharff & Coddington 1997 used when selecting taxa to include in their

analysis, was that the species which were scored should be typical for the genus, or at least an accepted part of the genus. Throughout the genus *Poltys* there is considerable variation in eye arrangements, in presence or absence of a scape on the female epigynum and in some endemic Australian species, presence or absence of a terminal apophysis in the male pedipalp (Smith unpub. data). These are all used as generic characters in this data matrix, yet vary within this genus. Consequently, it is possible that the genera which appear as potential relatives in the scenario above might be different if one of the more aberrant *Poltys* species were used instead. Here, *P. illepidus*, in addition to being the type species, was judged to be the most useful exemplar as it seems to exemplify the 'basic' *Poltys* body plan, and lacks some of the apparently more

derived characters seen elsewhere in the genus.

The second aim of this study was to test whether the taxa formerly included in the Poltyni would appear as a group when included with the taxa analysed by Scharff & Coddington. Even ignoring *Homalopollys*, which appears to be a tetragnathid (Smith unpub. data), it is extremely unlikely that the remaining taxa form a monophyletic grouping, although they may all occur scattered among a broader group of araneines. *Cyphalonotus* is the most consistently placed of these taxa, close to *Araneus*, and *Ideocaira* may also belong in the same area of the araneines (Scharff & Coddington 1997 clade 57). *Micropollys* may belong in the sister clade to these two (which would be clade 62 in Scharff & Coddington 1997, fig. 82), and, as already discussed, *Poltys* may belong in or near the '*Hypsosinga* clade'. However, given the limitations of this study noted above, these preliminary findings should be subjected to further analysis when the opportunity becomes available.

#### ACKNOWLEDGMENTS

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## A FOSSIL HARVESTMAN (ARACHNIDA, OPILIONES) FROM THE MISSISSIPPIAN OF EAST KIRKTON, SCOTLAND

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**ABSTRACT.** A fossil harvestman (Arachnida, Opiliones) from the Mississippian (Viséan: Brigantian) of East Kirkton, Scotland is described as *Brigantibunum listoni* new genus and species. At ca. 340 Ma, it represents the second oldest record of Opiliones. Although some details are lacking, this long-legged, small-bodied and rather gracile harvestman is surprisingly modern-looking and appears to show the impression of an annulate ovipositor. Its leg anatomy closely matches that of some living Eupnoi and it is tentatively referred to this clade. Like the newly discovered Rhynie chert harvestmen, it reinforces the idea that modern, crown-group Opiliones can be traced back to at least the mid-Paleozoic.

**Keywords:** Taxonomy, new species, Viséan, Paleozoic, Eupnoi

Fossil harvestmen (Opiliones) are very rare. Although they are best known from Tertiary ambers (e.g., Cokendolpher & Poinar 1998; Staręga 2002; Dunlop & Giribet 2003), there are also two Mesozoic records (Roger 1946; Jell & Duncan 1986) neither of which have been formally named and the first of which is dubious. Until recently the earliest harvestmen were Pennsylvanian (ca. 300 Ma) fossils from the Coal Measures of Commentry in France (Thevenin 1901) and Mazon Creek in the USA (Petrunkévitch 1913). Restudy of Petrunkévitch's (1913) putative extinct order Kustarachnida has shown that these Mazon Creek arachnids are misidentified harvestmen (Beall 1986, 1997; Dunlop 2004a). Additional Pennsylvanian-aged harvestmen have been collected from Missouri, USA (Dunlop 2004b) and Poland (Maciek Kania, pers. comm., 2004).

The oldest recorded harvestmen are exceptionally preserved, three-dimensional fossils from the Early Devonian (ca. 400 Ma) Rhynie cherts of Scotland (Dunlop et al. 2003, 2004). Provisionally assigned to the Eupnoi clade as *Eophalangium sheari* Dunlop et al. 2004, this exquisite, silicified material displays details of internal structures such as genitalia and trachea, all of which point towards these ancient

harvestmen having a very similar gross morphology to living animals. The second oldest harvestman is also rather modern looking and comes from the Mississippian (ca. 340 Ma) of East Kirkton in Scotland (Wood et al. 1985). The East Kirkton harvestman (Figs. 1–3) is preserved in a more typical fashion as a flattened impression and superficially resembles living 'daddy long-legs' forms. In general, Mississippian arachnid fossils are far less common than either Devonian or Pennsylvanian examples (see Dunlop & Rößler 2003 for a review), thus any record from this time period is significant.

The East Kirkton harvestman was briefly mentioned, with a figure, in the original summary paper dealing with the locality (Wood et al. 1985). It has also been noted or listed in some further publications (Smithson 1989; Selden 1993a, b; Clack 1998; Jeram 2001; Dunlop & Rößler 2003; Dunlop 2004a). Here we formally describe and name this important specimen and discuss its significance in the light of other recent fossil harvestman discoveries.

### METHODS

The East Kirkton harvestman was borrowed on research loan from the Hunterian Museum,



Glasgow, United Kingdom (GLAHM A2854), where it is customarily on display. The specimen was digitally photographed using a Leica DC100 digital camera mounted on a Leica MZFLIII microscope and drawn using a camera lucida attachment. Adobe Photoshop Limited Edition 5.0 was used to manipulate the digital images. For comparative purposes the type material of *Nemastomoides longipes* (Petrunkévitch 1913) from the Peabody Museum, Yale (YPM 171), *N. depressus* (Petrunkévitch 1913) from the United States National Museum (USNM 37974) and *Kustarachne tenuipes* Scudder 1890 (USNM 37967) was examined, along with *Eophalangium sheari* from Rhynie (held in the University of Munster, Germany) and extant species preserved in the Museum für Naturkunde Berlin.

**Geological setting.**—The East Kirkton Limestone is a fossil Konservat-Lagerstätte located near Bathgate, West Lothian, Scotland; about 27 km west of Edinburgh. The limestone is the lowest of five which occur within the Bathgate Hills Volcanic Formation. This in turn can be correlated with the lower part of the Brigantian Stage of the Viséan Series of the Mississippian (= Lower Carboniferous in European terminology). The Brigantian Stage spans the time interval 336.0–339.4 Ma. Further details can be found in Rolfe et al. (1994). The East Kirkton locality has also yielded scorpions (Jeram 1994, 2001), myriapods (Shear 1994) and a variety of terrestrial tetrapods including the anthracosaurid *Silvanerpeton miripedes* and the famous stem-amniote *Westlothiana lizziae*; however early insects and arachnid groups like the extinct order Trigonotarvida, which are usually fairly common in terrestrial deposits of this age, are so far absent.

**Preservation.**—GLAHM A2854 is preserved as a compression fossil on the surface of a thin, grey bed of calcareous tuff. The light red-brown coloration of the harvestman is analogous to that of the scorpion fossils etched from the East Kirkton limestone (Jeram 1994) and suggests that some constituent of the original cuticle still remains, rather than it being a wholly carbonized cuticle. This in turn suggests that chitinoclastic bacteria were excluded from the preservational environment during the formation of the deposit and the arthropod fossils contained therein. The fossil originated from bed 82 (S.P. Wood pers.

comm. 2002). Rolfe et al. (1994) identified the combined thickness of bed 81 and bed 82 (with a lateral variation in thickness between 80 and 140 mm) as the same unit which Geikie (1861) named 'bed b'. This unit contains dense accumulations of ostracods on some bedding surfaces as well as charcoallified plant material. This is also the likely source bed of the holotype of *Westlothiana lizziae*. Durant (1994) summarized the likely paleoenvironment in which the sediments exposed in the East Kirkton Quarry were deposited in a shallow lake close to the flanks of an active volcano. Volcanic eruption products including ash and tuffs, were eroded and washed down into the lake. Set against a backdrop of active volcanism in the area in which it formed, it is no surprise that ashy bands, pyroclastic fragments and chemical sediments influenced by hot spring activity dominate the sequence hosting both terrestrial and aquatic plant and animal fossils. Widespread development of limestone formed from stromatolitic algae also point to an unusual physio-chemical environment for the formation of this deposit.

In the fossil's plane of compression at least four elongate and articulated legs are preserved. A thin calcite vein cross-cuts the legs of the fossil (Figs. 1, 2). Close study of the harvestman body suggests that other legs may have broken off prior to preservation. However, it is obvious that such delicate structures, which easily break off in extant animals even while still alive, indicate only a short period of transport into the preservational environment. Perhaps this animal was rafted out onto the open lake on floating vegetation before dropping into the water?

#### MORPHOLOGICAL INTERPRETATION

**Body.**—The body (Figs. 1–3) is small and rounded. We suspect it is essentially a dorso-lateral to ventro-lateral compression in which the two sides of the body have become superimposed. As is typical for harvestmen, the prosoma and opisthosoma are broadly joined. Features such as eyes or mouthparts are equivocal, even under higher magnification, but the body does come to a slight, angular point on the dorsal side where an eye tubercle might be expected. Low-angle lighting reveals lines on the harvestman body which might correspond to the original opisthosomal segmentation and/or elements of the coxae which



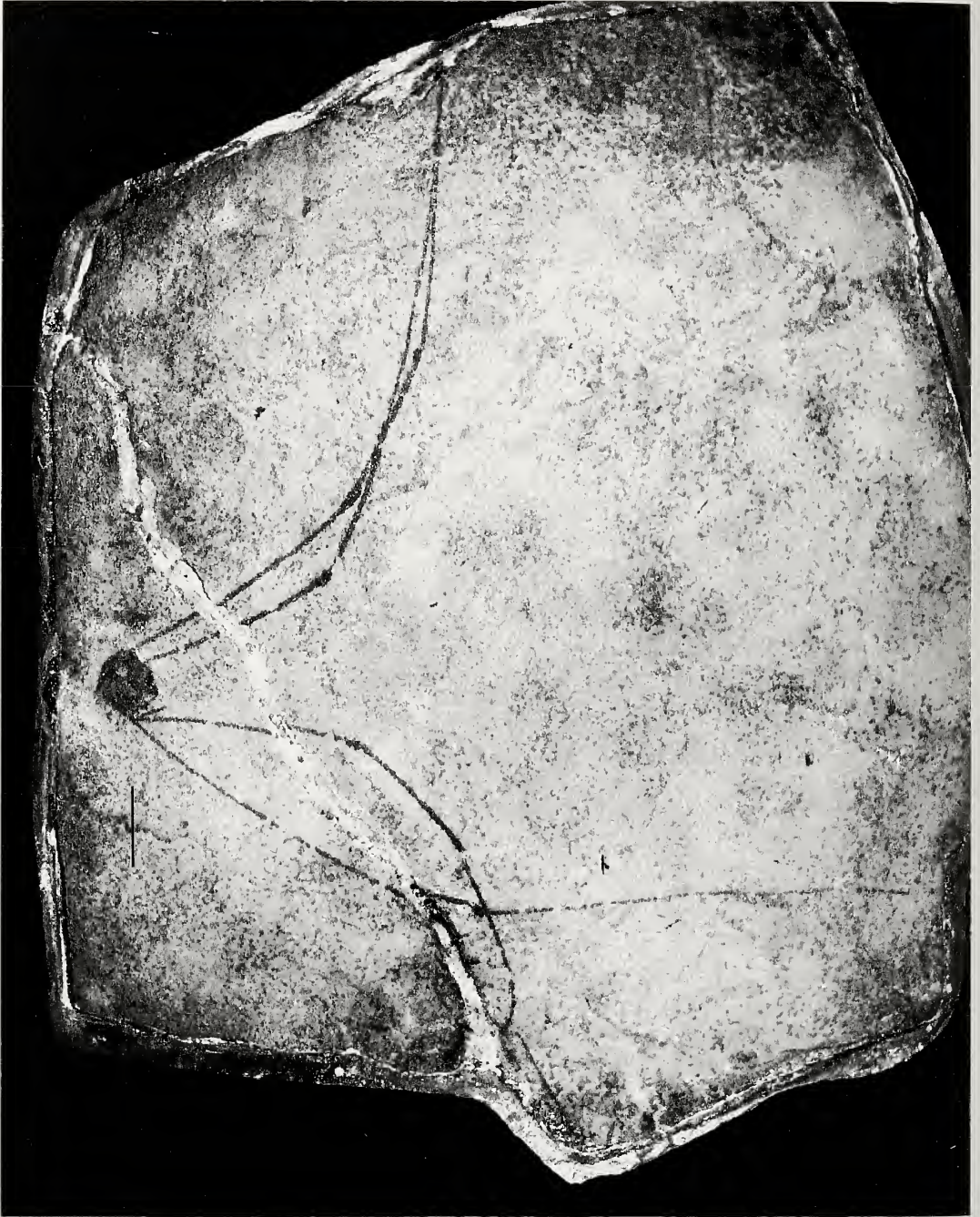


Figure 1.—*Brigantibunum listoni* new genus and species. from the Mississippian (Viséan: Brigantian) of East Kirkton, Scotland. This modern-looking specimen is here tentatively assigned to the Eupnoi clade. Scale bar = 5 mm.

come up the side of the body in many living harvestmen. These lines do not form a clear pattern running the length of the body and in similar-looking extant harvestmen segmentation is generally poorly defined (e.g.,

Shultz 2000) and may only be betrayed by folds or color patterns on the body surface. The fossil also reveals fine tuberculation on the body where cuticle has been preserved and, while there is some degree of locali-



zation, the tubercles do not define identifiable segments.

**Ovipositor.**—One intriguing feature is an apparently annulate structure overlaying the left side of the body, which is only clearly visible under high magnification and low angle lighting (Fig. 3). It is associated with original cuticle which tends to suggest it is not an artefact, and at least towards the 'dorsal' end there are rows of tiny circular structures across each annulation which might be tubercles or setal sockets. We tentatively interpret this structure as an ovipositor since its annulate morphology and proportions relative to the body are suggestive of that in a modern eupnoid harvestman (e.g., Shultz 2000). The East Kirkton scorpions preserve respiratory organs (Jeram 1994), which shows that there is the potential at this locality to recover internal features. If this is an ovipositor, it is the second oldest record of internal genitalia, after the one recovered in *Eophalangium sheari* from Rhynie (Dunlop et al. 2003, 2004). It implies that the East Kirkton fossil is a female which probably laid its eggs in the substrate. In living harvestmen the ovipositor is apparently extended through hemolymph pressure (Shultz 2000). Perhaps the ovipositor in the fossil was squeezed out of the body during compression and came to lie across the opisthosoma?

**Legs.**—Four almost complete legs are preserved, all of which are very long and gracile; up to ca. twelve times the length of the body. A small fragment of either a fifth leg or, perhaps, a pedipalp is also preserved. It is difficult to assign legs unequivocally to their sequence in the body, but the longest leg (which is also the most gracile) is probably leg 2. This leg is longest in most living (non-cyphophthalmid) harvestman and has a more tactile function. Indeed all 4 preserved legs express slightly different femur lengths (see Systematics) and this might indicate that the fossil is essentially a lateral view preserving legs 1–4 on one side of the body; with the corresponding legs from the other side either missing or still within the matrix. A tentative numbering scheme is proposed based on this assumption (Fig. 2).

Discrete podomeres can be recognized, and the basic leg anatomy is a precise match for living eupnoid harvestmen (cf. Shultz 2000). The femur is elongate and slender. It is fol-

lowed by a very short patella which is slightly thicker than the adjacent podomeres. It forms a distinct and bulbous 'knee'. The tibia is again elongate and slender, widening distally to form a disjunct articulation with the next podomere, the basitarsus. This basitarsus is also long and slender, although the transition to the telotarsus is indistinct. In many living harvestmen the telotarsus is composed of many short tarsomeres. These cannot be resolved in the fossil, but the distal curvature of at least one of the legs (leg 1 in our scheme, see Figs. 1 & 2) implies that it, too, was formed from numerous articulating elements. Claws at the ends of the legs (the apotele) are equivocal.

## SYSTEMATIC PALAEONTOLOGY

### ?Eupnoi Hansen & Sørensen 1904

**Remarks.**—As noted by Selden (1993a), the East Kirkton fossil is clearly a harvestman, but explicit diagnostic characters of higher taxa within Opiliones are not clearly preserved. Nevertheless, its overall morphology with a 4 mm globular body and long, essentially homogeneous legs is wholly inconsistent with Cyphophthalmi, which are tiny (typically 1–2 mm) with short, stubby legs. Nor does it resemble the more robust Laniatores in which leg 4 is often enlarged and spiny (although not, for example, in oncopodids) and in which prominent, raptorial pedipalps would be expected. This leaves the Palpatores group, the monophyly of which is currently in dispute (compare Shultz 1998 and Giribet et al. 2002). The older Rhynie chert harvestmen preserve convincing eupnoid characters (Dunlop et al. 2003, 2004a), thus both Eupnoi and its putative sister taxon lineage, Dyspnoi sensu Shultz (1998) or (Dyspnoi + Laniatores) sensu Giribet et al. (2002), can be predicted from the Mississippian.

Both the Eupnoi and Dyspnoi clades, which make up the traditional Palpatores group, include long-legged taxa. The extremely long and gracile legs in GLAHM A2854, which are up to about twelve times body length, tend to favor affinities with phalangiid or sclerosomatid harvestmen (Eupnoi), for example members of common eupnoid genera like *Leiobunum* C.L. Koch 1839, *Opilio* Herbst 1798 and *Phalangium* Linnaeus 1758. Among the Recent Dyspnoi, common genera such as

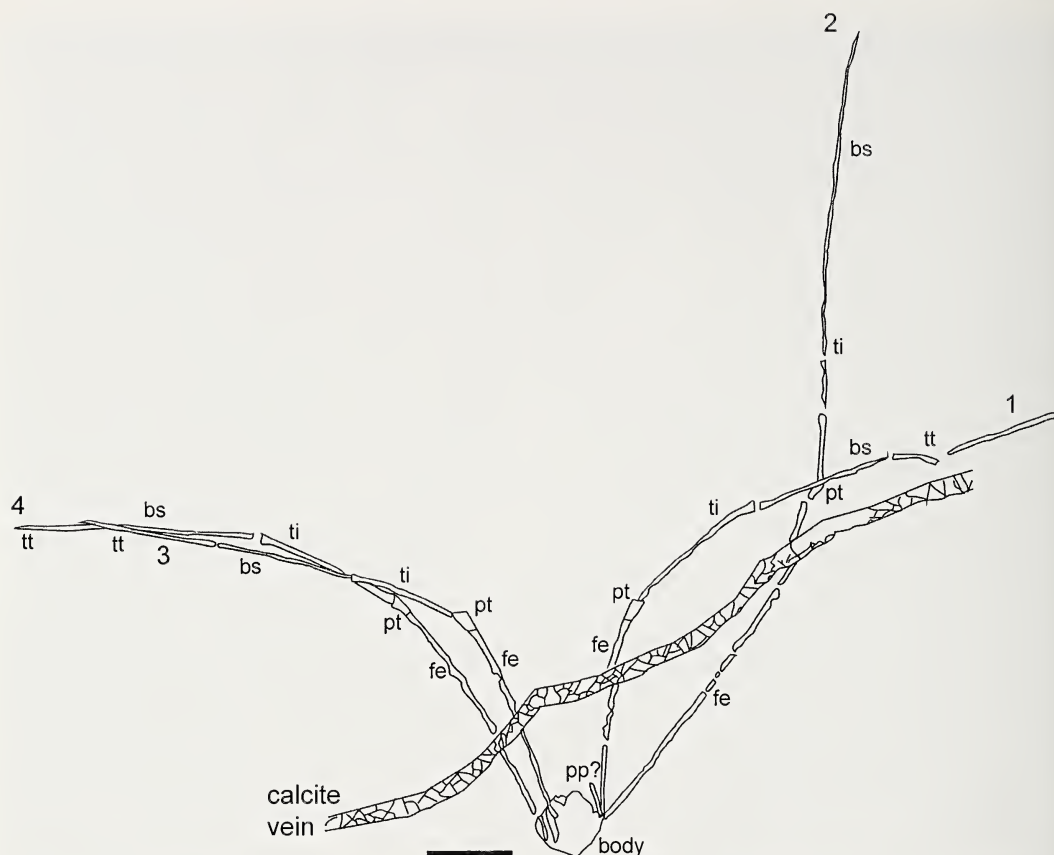


Figure 2.—Interpretative drawing of the specimen shown in Fig. 1. Abbreviations: bs = basitarsus, fe = femur, pp = possibile pedipalp, pt = patella, ti = tibia, tt = telotarsus. Legs tentatively numbered from 1 to 4, with leg 2 longest. Scale bar = 5 mm.

*Nemastoma* C.L. Koch 1836 and *Dicranolasma* Sørensen 1873 typically have legs which are somewhat shorter in relation to body length. Members of the dyspnoid genus *Mitostoma* Roewer 1951 are closer to GLAHM A2854 in terms of leg lengths. Data from the fairly widespread *M. chrysomelas* (Hermann 1804) in Martens (1978, p. 143) suggests that leg length (13.7 mm) is, at best, about eight times body length (1.7 mm), although in a highly-specialized Alpine cave species like *M. anophthalmum* (Fage 1946) leg length (22.8 mm) can be over fourteen times body length (1.6 mm); data from Martens (1978, p. 149). Clearly leg length is not an ideal character and as noted by Martens, these parameters can vary even within a species and between males and females.

The putative ovipositor also hints at a eupnoi. If our interpretation is correct, this annulate morphology only occurs in Cypho-

phthalmi (rejected for the reasons outlined above) and Eupnoi (Shultz 1998, 2000; Giribet et al. 2002). However, explicit autapomorphies of Eupnoi cannot be resolved unequivocally in the fossil. The lakeside paleoenvironment is unlikely to have trapped either high mountain and/or cave animals. The long and gracile legs in the fossil are more characteristic for certain phalangiid and sclerosomatid eupnoids, as opposed to the usual range in non-specialist dyspnoids. On these grounds we tentatively assign the East Kirkton fossil to Eupnoi.

#### *Brigantibunum* new genus

**Type and only species.**—*Brigantibunum listoni* new genus and species.

**Etymology.**—From the Brigantian age of the fossil and the suffix “bunum” used in modern genera of small bodied, long-legged harvestmen such as *Leiobunum*.



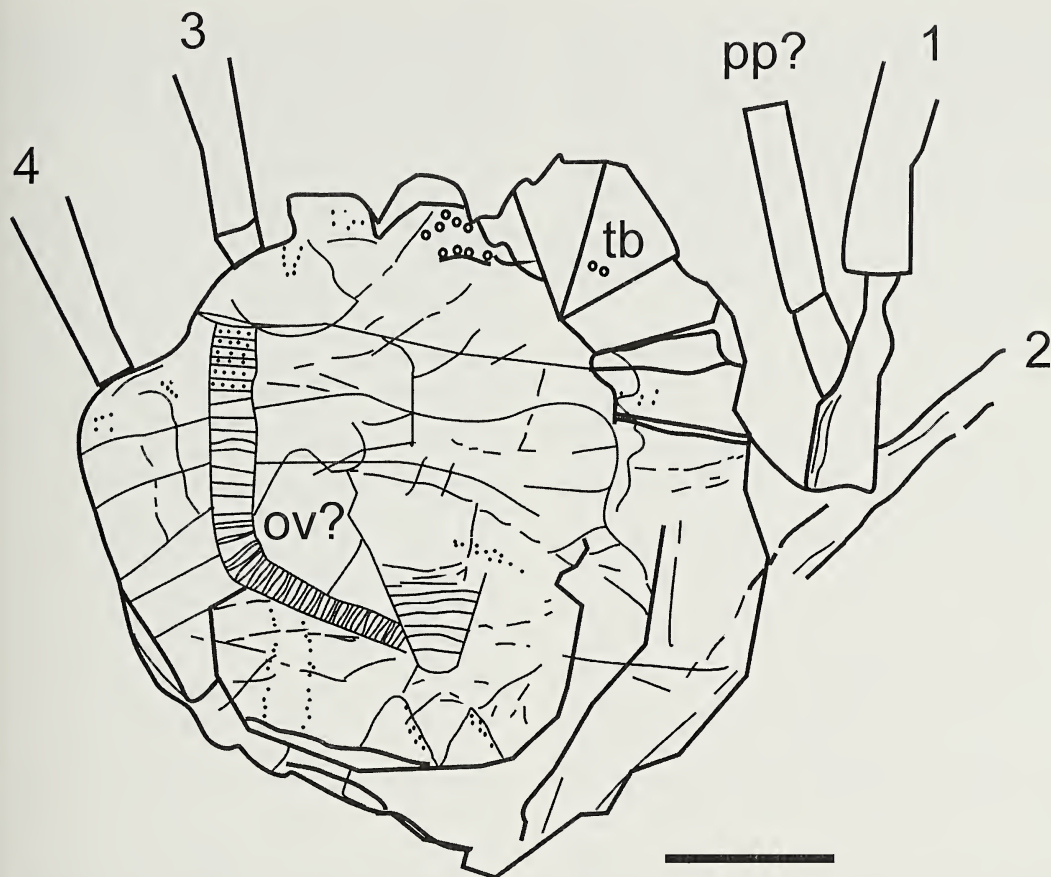


Figure 3.—Detail of the body region under low angle lighting and immersion in alcohol. Abbreviations: ov? = possible annulate ovipositor, tb = tuberculation of cuticle. Leg sequence as in Fig. 2. Scale bar = 1 mm.

**Diagnosis.**—Extremely gracile Paleozoic harvestman with long, slender legs up to twelve times the length of the small, ovate body. Femora at least two and a half to three times the length of the body.

**Remarks.**—The *Eophalangium sheari* material from the Devonian of Rhynie, Aberdeenshire, Scotland includes a long-legged specimen. Given the very different modes of preservation, direct comparisons with the East Kirkton fossil are problematic. The three-dimensional Rhynie material yields many characters not testable in the East Kirkton specimen. Furthermore, the (male) Rhynie fossil associated with the long legs is incomplete and the full extent of both the legs and body remains equivocal. Further discoveries may change this interpretation, but we can find no explicit autapomorphies or even reliable ratios of body proportions to argue that the East

Kirkton fossil belongs to *Eophalangium* Dunlop et al., 2004.

Among the Pennsylvanian opilionids, our fossil is clearly not congeneric with the putative Commeny trogluoid *Eotrogulus fayoli* Thevenin 1901, which is a robust animal with an elongate body and comparatively short legs. This leaves three species of *Kustarachne* Scudder 1890, two of which are rather incomplete and doubtful, and three species of *Nematostomoides* Thevenin 1901; of which *N. depressus* from Mazon Creek is a misidentified phalangiotarbid (Beall 1997; pers. obs.). The East Kirkton fossil appears longer-legged than all these Pennsylvanian forms, although the Mazon Creek specimens are in nodules and the full extent of the legs is, of course, not preserved. In detail, the length of the femur offers a potential diagnostic character and the femora in the East Kirkton fossil are pro-

portionately longer (ca. 3 times body length) than the femora in *Nemastomoides* and *Kustarachne* (ca. 1–2 times body length). Overall, GLAHM A2854 is a unique find and the only record of a Mississippian harvestman. It most closely resembles the Commeny species *N. elaveris* Thevenin 1901, but based on its extreme leg length and gracile appearance we assign it to a new genus diagnosed on the body–femur ratio.

***Brigantibunum listoni* new species**

Figs. 1, 2.

?Earliest known harvestman (Arachnida, Opiliones): Wood et al. 1985: 355–356, fig. 1.

Opilionid or harvestman: Smithson 1989: 676–678; Selden 1993a: 392–393; Selden 1993b: 305–306; Clack 1998: 66–69; Jeram 2001: 374, tabs. 16.1, 16.2; Dunlop & Rößler 2003: 389; Dunlop & Giribet 2003: 371; Dunlop 2004a: 24; 2004b: 67.

**Type.**—Holotype, from the East Kirkton Quarry, near Bathgate, (27 km west of Edinburgh), West Lothian, Scotland (Grid reference NS 991690), collected by Mr. Stan P. Wood, derived from Unit 82 of the East Kirkton Limestone, West Lothian Oil-Shale Formation, Strathclyde Group, Upper Viséan (Brigantian), Mississippian (= Lower Carboniferous in European stratigraphy) (GLAHM A2854).

**Etymology.**—For Jeff Liston (University of Glasgow & Hunterian Museum).

**Diagnosis.**—As for the genus.

**Description.**—Body small, rounded, ca. 4 mm in diameter. Red–brown cuticle includes fine tuberculation and possible segment/coxal boundaries. Elongate, annulate structure (?ovipositor), length 2.5 mm, curves across body on left side. Small, incomplete limb element (?pedipalp), length 2 mm, projects from body on right side. Four legs preserved, all long, slender and extremely gracile. All legs with different lengths and podomere proportions, tentatively numbered in sequence (see also Morphological interpretation) from longest to shortest: 2 4 1 3. All legs slightly curved, one leg (probably leg 2) distinctly longer; maximum approximate preserved leg lengths as follows. Leg 1: 38 mm, leg 2: 51 mm, leg 3: 34 mm, leg 4: 40 mm. Femora long, lengths as follows. Leg 1: 12 mm, leg 2: 21 mm, leg 3: 11 mm, leg 4: 14 mm. All patellae short, ca. 1.5 mm. Tibiae longer, lengths as follows. Leg 1: 8 mm, leg 2: 14

mm, leg 3: 6 mm, leg 4: 9 mm. Basitarsi lengths as follows. Leg 1: 8 mm, leg 2: unclear, leg 3: 8 mm, leg 4: 9 mm. Telotarsi incomplete, but long and slender.

## DISCUSSION

*Brigantibunum listoni* fits into a developing pattern (e.g., Dunlop et al. 2003, 2004; Dunlop 2004a, b) in which harvestmen appear to have evolved relatively early into recognizable crown-group forms (i.e. animals assignable to clades with Recent representatives) and exhibit a high degree of stasis, with little fundamental change over hundreds of millions of years. Harvestmen with the same basic shape as the East Kirkton fossil, remain common and abundant today; particularly in the northern hemisphere. To put this into context, the oldest crown-group spiders (Selden 1996) are mesotheles (the most basal living spider clade) and are first recorded from the end of the Pennsylvanian. This is some 100 million years after the oldest crown-group harvestmen from Rhynie, which can be assigned to the eupnoids; a somewhat derived clade. It is also worth mentioning that in recent arachnid phylogenies (e.g. Giribet et al. 2002) harvestmen seem to resolve in a fairly basal position (compared to spiders) as part of the so-called Dromopoda clade along with scorpions, pseudoscorpions and solifuges.

## ACKNOWLEDGMENTS

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## A REVISION OF THE SPIDER GENUS *TAURONGIA* (ARANEAE, STIPHIDIOIDEA) FROM SOUTH-EASTERN AUSTRALIA

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**ABSTRACT.** The spider genus *Taurongia* Hogg 1901 and the species *T. punctata* (Hogg 1900) are redescribed. *Taurongia punctata* is shown to be a rather variable species with a widespread distribution across the eastern central Victorian highlands. *Taurongia punctata* is a robust spider, contrasting with a more gracile new species, *T. ambigua*, described from the western Victorian highlands. The placement of the latter in *Taurongia* is provisional and may change once other undescribed ‘*Taurongia* group’ genera from eastern Australia have been examined. The *Taurongia* species dealt with here differ from the latter taxa in having an increased number of cylindrical spigots and a large palpal median apophysis.

**Keywords:** Taxonomy, cribellate, new species

Hogg (1900) described two ‘dictynid’ spiders from central Victoria under the name *Hylobius*. This name (preoccupied in Coleoptera) was subsequently replaced by *Taurongia* (Hogg 1901). Lehtinen (1967) characterized the genus, figuring *T. punctata* (Hogg 1900), and placed it in his Desidae, Desinae. Forster (1970) noted that the available data were insufficient for accurate placement of *Taurongia* in his concept of the Desidae. *Taurongia* has long been confused with related ‘*Taurongia* group’ taxa that are widely distributed in eastern Australian forests from Tasmania to Queensland. These taxa comprise several undescribed genera that are morphologically diverse but united by characteristics of the genitalia, notably the palpal tegular structure and the placement of the median apophysis (reduced to a slender, spine-like process in most taxa, except *Taurongia*). Here, the genus *Taurongia* is reviewed as a step toward characterizing this group of spiders and clarifying their relationships.

### METHODS

Specimen examinations, measurements and drawings were made using a Wild M5 or Leica M12 microscope with graticule and drawing attachment. Epigynal preparations were cleared in lactic acid, before mounting in glycerol for microscopic examination. The left side male palp is illustrated. Specimen preparations for scanning electron microscopy

were taken through 80–100% alcohol stages, 100% acetone and then air dried.

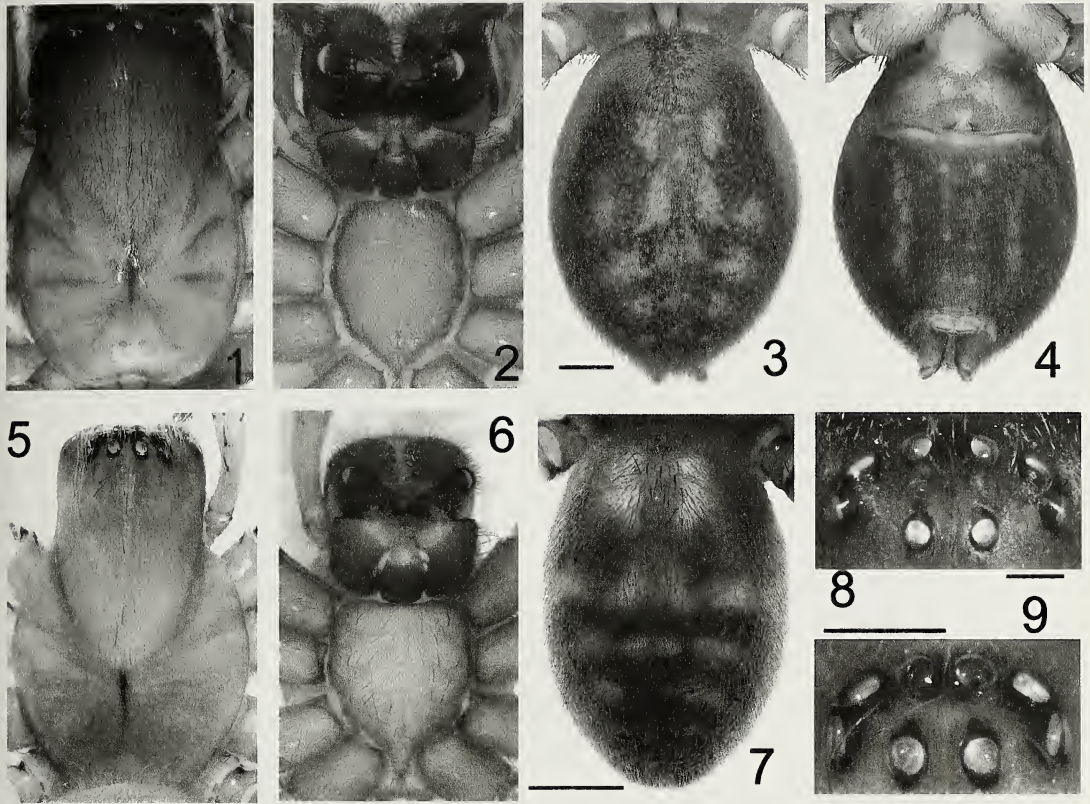
**Abbreviations and definitions.**—“Tegular window” refers to the gap between the proximal embolus and the basal part of the conductor. BL = body length; CL = carapace length; CW = carapace width; CapW = caput width; LL = labium length; LW = labium width; SL = sternum length; SW = sternum width; EGW = eye group width; AME = anterior median eyes; ALE = anterior lateral eyes; PME = posterior median eyes; PLE = posterior lateral eyes; MOQ = median ocular quadrangle; RTA = retrolateral tibial apophysis; RVTA = retroventral tibial apophysis; MA = median apophysis; ALS = anterior lateral spinneret; PMS = posterior median spinneret; PLS = posterior lateral spinneret; MAP = major ampullate spigot; mAP = minor ampullate spigot; Cyl = cylindrical spigots; Pc = paracribellar spigots; mPLS = modified PLS spigot; n = nubbin. The material examined in this study is lodged in the following repositories: AM = Australian Museum, Sydney; NHM = Natural History Museum, London; NMV = Museum of Victoria, Melbourne; WAM = Western Australian Museum, Perth.

### TAXONOMY

Superfamily Amaurobioidea Thorell 1870  
*Taurongia* Hogg 1901

*Hylobius* Hogg 1900: 82 (preoccupied by *Hylobius* Germar 1817).





Figures 1–9.—*Taurongia* species: 1–4, 8. *T. punctata* (Hogg); 5–7, 9. *T. ambigua* new species. 1, 5. Carapace; 2, 6. Sternum and mouthparts; 3, 4, 7. Abdomen, 3, 7. dorsal; 4. ventral; 8, 9. Eyes, anterodorsal. Scale bars: 1 mm (Figs. 1–4, 5–7); 0.5 mm (Figs. 8, 9).

*Taurongia* Hogg 1901: 278 (replacement name); Lehtinen 1967: 267, 326; Platnick 2004.  
*Hylobihoggia* Strand 1935: 304 (superfluous replacement name); Lehtinen 1967: 267; Platnick 2004.

**Type species.**—*Hylobius divergens* Hogg 1900 by original designation, currently a junior synonym of *Hylobius punctatus* Hogg 1900.

**Comment on synonymy of type species.**—Hogg (1900) described two species in his genus *Hylobius* and designated *H. divergens* as the type. In 1901 he replaced the pre-occupied generic name with *Taurongia*. Hogg's material came from the Macedon District in Victoria. It comprised the female holotype of *Taurongia divergens* and the male and female syntypes of *T. punctata*, although Lehtinen (1967) noted that the female syntype was a juvenile specimen. Lehtinen (1967) placed *T. divergens*, the type species, in synonymy with *T. punctata*, presumably because

the male *T. punctata* specimen provided the better character set. Subsequent collecting by the author has not revealed a second species of *Taurongia* in the Macedon District.

**Diagnosis.**—Cribellate spiders with a robust or gracile body form. Carapace dark brown without obvious patterning. Male palp: cymbium digitiform, spinous; median apophysis large, spatulate; RTA large, ventrad. Epigynum divided by a median septum, or septum indistinct. PMS with 4–6 cylindrical sigpots.

**Redescription.**—Medium-large robust or gracile cribellate spiders. Carapace, jaws and legs dark reddish brown, anterior caput and jaws darkest; lateral carapace with dark radial streaks from fovea; legs not banded. Dorsal and lateral abdomen dark brownish-grey, with more or less distinct pallid chevrons dorsally, the 3 anterior pairs with small sigillae; venter grey, bounded laterally by pallid, dotted lines,



Figure 10.—Distribution of *Taurongia punctata* (closed squares) and *T. ambigua* (open circle).

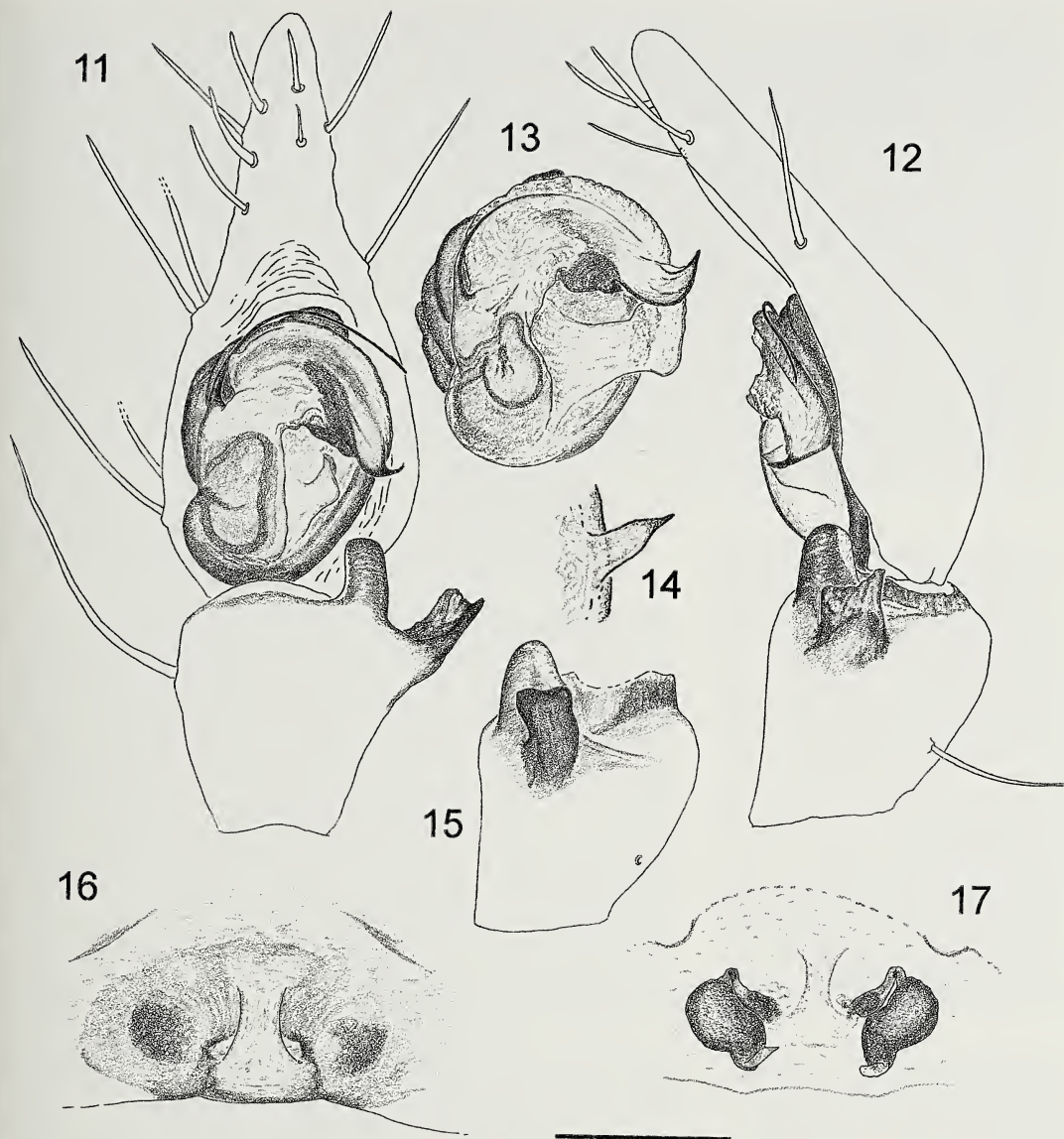
with two lines of paired spots medially (Figs. 1–4, 7).

Body and leg hairs plumose, feathery hairs absent. Carapace with prominent caput; profile moderately arched, highest in mid-caput region; foveal slit moderately long and deep, curving down onto concave rear slope of carapace (Figs. 1, 5). Clypeus wide, ca.  $3 \times$  width of an AME, anterior margin strongly convex. Chilum an undivided, median plate. Eyes eight, AME or PME smallest (Figs. 8, 9). Eye group moderately narrow, EGW ca.  $0.50\text{--}0.60 \times$  width of caput; eyes in two rows, from above AER recurved, PER procurved-straight; MOQ longer than wide, slightly narrower anteriorly. PME, PLE and ALE with canoe-shaped tapeta. Cheliceral paturon robust, proximally kneed, with large boss; fangs strong, short; fang groove short (Fig. 2, *T. punctata*); paturon and fangs more gracile and longer in *T. ambigua* (Fig. 6). Two adjacent retromarginal teeth (sometimes set in paler area of cuticle); and 3 adjacent promarginal teeth, last tooth extended as a strong carina; retromargin with one long modified seta near base of fang, several modified setae above promargin. Maxillae broad, longer than wide, lateral margins convex with a strong antero-lateral linear serrula. Labium longer than wide, widest anterior to baso-lateral excava-

tions, narrowing to a weakly concave apex. Sternum cordate, longer than wide, shortly to strongly pointed between coxae 4 (Figs. 2, 6). Legs 14/23, with inclined and vertical hairs. Trochanters slightly to strongly notched. Retrocoxal hymen absent. Three tarsal claws, superior 9–11 teeth, inferior 2–3 teeth; claw tufts and scopulae absent but ventral tarsi and metatarsi 1–4 strongly hirsute in *T. punctata*, much less hirsute in *T. ambigua*. Female palpal tarsi spinose; palpal claw with 11–12 teeth. Trichobothria increasing in length distally, in single row on tarsi (6–7) and metatarsi (5–6); two rows on tibia; present on male and female palpal tarsus and tibia. Bothria collariform, proximal plate with weak to well defined longitudinal ridges (Figs. 31, 35). Tarsal organ placed distal to trichobothria, capsule with an ovoid, more or less key-hole shaped pore (Figs. 32, 36). Calamistrum: ca.  $0.4 \times$  length of metatarsus, subcentrally to proximally placed, with a dorsally contiguous field of recumbent setae; delimited at each end by a retrodorsal spine.

*Male palp* (Figs. 11, 12, 37, 38): Cymbium with a digitiform apex with several bristles and spines. Bulb subcircular to ovoid. Tegulum with a narrow prolateral-basal sclerotised region within which the sperm duct runs in an ovoid loop, and from which the conductor





Figures 11–17.—*Taurongia punctata*. 11–15. Male palp. 11, 12. Palp, ventral, retrolateral; 13. Bulb, ventral (Mt Donna Buang); 14. Median apophysis (Mt Buller); 15. Tibia, retrolateral (Woodend). 16, 17. Epigynum, ventral, dorsal. Scale bar: 0.25 mm

arises anteriorly; and a large retrolateral-basal membranous region from which the MA arises basally. MA usually large, membranous and hyaline, often ‘spatula-shaped’; less commonly reduced in size (Fig. 14). Embolus spiniform, curving in a semicircle from its prolateral tegular origin around the conductor margin. Small tegular window present at embolus/conductor base. Conductor weakly T-shaped, with a short, membranous stalk supporting a semicircular–falciform head with a

marginal embolic groove, narrowing retro-distally as a reflected or elongate tip (Figs. 11, 37). Tibia about as long as wide, with two distal apophyses, the RVTA and a ventrad placed RTA. Patella about as long as wide with a dorsal bristle.

*Epigynum:* Fossa divided by a distinct median septum expanding posteriorly into a posterior lobe (Fig. 16), or fossa open and septum indistinct (Fig. 39). Lateral teeth absent. Copulatory ducts narrow, very short or simply

coiled, opening postero-laterally (Figs. 17, 41). Paired spermathecae ovoid, well separated, placed lateral to copulatory duct openings at posterior end of fossa.

Tracheal system simple, with four unbranched tracheal tubes confined to the abdomen. Spiracle just anterior to cribellum, about  $0.4 \times$  as wide as cribellum plate (Fig. 18). Spinnerets: PMS with 4–6 cylindrical spigots (Fig. 20).

**Included species.**—*Taurongia punctata* (Hogg), *T. ambigua* new species.

**Comments.**—The new species described here, *T. ambigua*, is attributed to *Taurongia* largely on the basis of its similarities to the type species in genitalic and spinneret characters (similar cymbial, tegular and MA structure; relatively simple copulatory ducts; increased numbers (4–6) of cylindrical spigots on PMS (only 1 or 2 spigots present in related taxa (pers. obs.)). However, there are also significant differences in body build, eye sizes, trochanteral notches and cuticular sculpturing, which make the placement of *T. ambigua* in *Taurongia* provisional.

*Taurongia punctata* (Hogg 1900)

Figs. 1–4, 8, 10, 11–23, 34–36

*Hylobius punctatus* Hogg 1900: 84, plate XII, fig. 3.

*Hylobius divergens* Hogg 1900: 82, plate XII, fig. 2.

*Taurongia punctata* (Hogg): Hogg 1901: 279; Lehtinen 1967: 267, figs. 122, 123, 127; Platnick 2004.

*Taurongia divergens* (Hogg): Hogg 1901: 279; Lehtinen 1967: 267 (placed in synonymy with *T. punctata*).

*Hylobihoggia divergens* (Hogg): Strand 1935: 304.

*Hylobihoggia punctata* (Hogg): Strand 1935: 304.

**Type material.**—*Hylobius punctatus*: lectotype (present designation) male (examined), 1 paralectotype juvenile female [not examined, noted by Lehtinen (1967)], Macedon District, Victoria, Australia, H.R. Hogg (NHM).

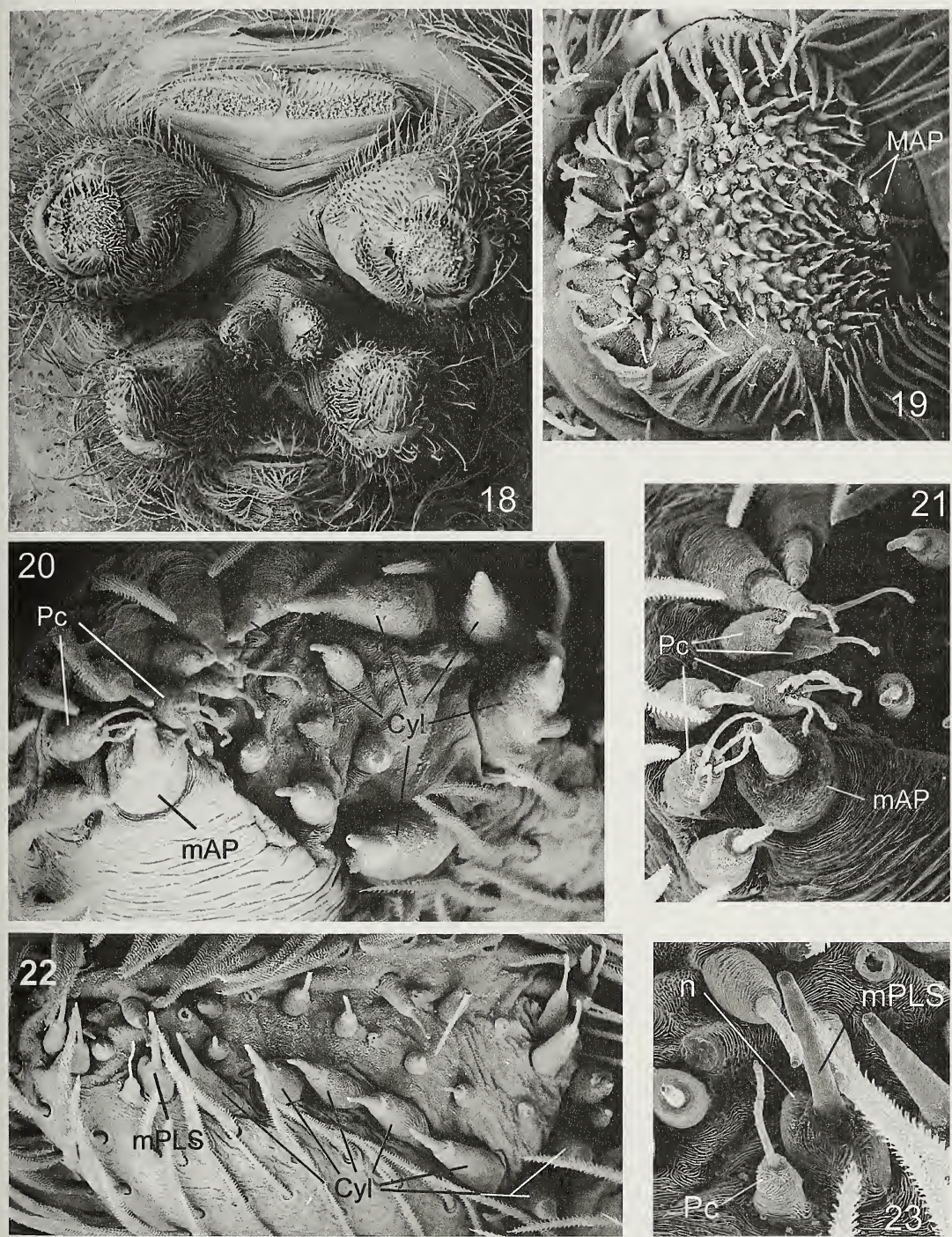
*Hylobius divergens*: Holotype female (examined), Macedon District, Victoria, Australia, H.R. Hogg (NHM).

**Other material.**—AUSTRALIA: Victoria: 1 ♂, 1 ♀, Sanitorium Picnic Ground Lake, Mt Macedon, 37°23'S 144°35'E, irregular sheet web on rotting log with egg sac, 23 February 1996, M. & A. Gray (AM KS45401); 1 ♀ same data as KS45401 (AM KS45403); 1 ♀, same data as KS45401 (no egg sac) (AM

KS45402); 1 ♀, same data as KS45402 (AM KS45404); 1 ♀, Mt Disappointment area, 37°26'S 145°08'E, 26 August 1973, M. Gray (AM KS34511); ♀, Warburton, 37°45'S 145°42'E, 8 September 1959, A. Neboiss (AM KS34512); 2 ♀, Mt Macedon, 37°23'S 144°35'E, rainforest, in rotting log, 14 March 1970, M. Gray (AM KS34513–14); 1 ♀, Blue Range Rd, 13 km S. of Thornton, 37°19'S 145°51'E, 9 April 1978, M.R. Gray (AM KS88187); 1 ♂, 1 ♀, 1 juvenile, Rubicon State Forest, 13 km S. of Thornton on Royston Rd via Rubicon, 37°19'S 145°51'E, 7 April 1978, M.R. Gray (AM KS88180); 2 ♂, data as for AM KS88180, collected as juveniles, matured July and August 1978 (AM KS88181–2); 1 ♂, 1 ♀, 7.5 km SE. of Woodend on Mt Macedon Road, 37°28'S 144°37'E, in log, 4 April 1978, M.R. Gray (abdomen of AM KS88176 used for SEM) (AM KS88176–77); 1 ♀, data as for AM KS88176 except 6 April 1978 (AM KS88179); 2 ♀, Omeo Highway 52 km N. of Omeo between Glen Wills and Sunnyside, 36°50'S 147°31'E, 13 April 1978, M.R. Gray (AM KS88188–89); 2 ♀, 3 km E. of Mirimbah on Mt Stirling Rd, 37°06'S 146°27'E, 8 April 1978, M.R. Gray (AM KS88183–84); 1 ♀, 7 km E. of Mirimbah on Mt Stirling Rd, 37°09'S 146°29'E, 920 m, irregular sheet web leading to retreat in crevice in bank, 8 April 1978, M.R. Gray (AM KS88185); 1 ♂, Box Corner, 4.5 km N. of Mt Buller Village, 37°07'S 146°26'E, 8 April 1978, 1000 m, M.R. Gray (AM KS88186); 1 ♂, Central Highlands, Forestry Rd 26, 0.2 km WNW. of Donna Buang Rd junction, 37°43'00"S 145°39'30"E, flight intercept trap, *Eucalyptus* forest, 21 January–7 April 1995, G. Milledge (NMV K6557); 1 ♂, Central Highlands, 0.7 km N of Acheron Gap, 7 km N. of Mt Donna Buang, 37°40'17"S 145°44'20"E, pitfall trap, *Eucalyptus* forest, 28 December 1995–21 February 1996, G. Milledge (NMV K6558); 1 ♀, The Beeches, 37°28'S, 145°49'E, 25 May 1991, M.S. Harvey, M.E. Blosfelds (WAM 98/2049); 1 ♀, Cumberland Falls, 37°34'S, 145°53'E, under log, 27 May 1991, M.S. Harvey, M.E. Blosfelds (WAM 98/1995).

**Diagnosis.**—Differs from *T. ambigua* by its more robust build, smaller eye size, absence of deep trochanteral notches, male palp with conductor apex strongly curved and epigynal fossa divided by a median septum.





Figures 18–23.—*Taurongia punctata*, spinnerets (female). 18. Spinneret field; 19. ALS (LHS); 20. PMS (RHS); 21. PMS, anterior area; 23. PLS (LHS), 24. mPLS and Pc spigots on apical PLS.



**Description.**—*Male (Mt Macedon, AM KS45401)*: BL 9.54, CL 5.67 (range 5.20–5.67), CW 3.87, CapW 2.98, EGW 1.66, LL 0.97, LW 0.79, SL 2.94, SW 2.29. Body robust, caput wide (Fig. 1). Eyes: smaller and eye group narrower (ca. 0.5 caput width) than in *T. ambigua*; PME smallest, ALE > AME  $\geq$  PLE > PME; AME weakly protuberant on a low common tubercle (Fig. 8). Sternum cordate, moderately long and shortly pointed posteriorly (Fig. 2). Legs: robust, relatively short, 1423 (I: 17.00; II: 15.07; III: 12.87; IV: 15.87); ratio tibia I length: CW = 1:0.93. Ventral tarsi and metatarsi moderately hirsute. Trochanters 1, 2 unnotched, 3, 4 slightly notched. Spination: I: femur d1-1-0-2, p0-0-2-0; patella 0; tibia v2-2-2, p1-1-1-0, r1-1-1-0; metatarsus d0-0-2, v2-2-1, p0-1-0-1, r0-1-0-1; tarsus 0; II: femur d1-2-0-2, p0-1-0-1; patella 0; tibia v2-2-2, p1-1-1-0, r1-1-1-0; metatarsus d0-1-2, v2-2-1, p1-1-0-1, r1-1-0-1; tarsus 0; III: femur d1-2-0-2, p0-1-0-1; patella 0; tibia d0-0-1-0-0, v1-2-2, p1-1-0-1-0, r1-1-0-1-0; metatarsus d0-1-2, v2-2-1, p1-1-1, r1-1-1; tarsus 0; IV: femur d1-1-0-2, p0-1-0-1; patella 0; tibia v1-1-2, p1-1-0-1-0, r1-1-0-1-0; metatarsus d0-1-2, v2-2-1, p1-1-1, r1-1-1; tarsus 0. Male palp (Figs. 11–15): distal conductor strongly tapered and curved to a short, spine-like apex; MA usually large and prominent; RTA a large ventrad, rectangular plate; RVTA thick, peg-like.

*Female (Mt Macedon, AM KS45402)*: BL 14.47, CL 7.27 (range 5.36–7.27), CW 4.87, CapW 4.00, EGW 2.07, LL 1.17, LW 0.97, SL 3.49, SW 2.76. Body, eyes and legs similar to male. Legs: 1423 (I: 17.73; II: 15.73; III: 13.40; IV: 16.53); ratio tibia I length to CW = 1:0.90. Cuticle surface smooth to weakly ridged. TO capsule smooth, pore ovoid with a short, narrow slit proximally (Fig. 36). Spination: I: femur d1-2-0-2, p0-0-2-0; patella 0; tibia v2-2-2, p0-1-1-1-0, r1-0-1-0-1-0-0; metatarsus d0-0-2, v2-2-1, p0-1-1-0-1, r0-0-1-0-1; tarsus 0; II: femur d1-2-2, p0-1-1; patella 0; tibia v2-2-2, p1-1-1-0, r1-1-1-0; metatarsus d0-0-2, v2-2-1, p1-1-0-1, r1-1-0-1; tarsus 0; III: femur d1-2-2, p0-1-1; patella 0; tibia d1-0-1-0-0, v1-1-2, p1-1-0-1-0, r1-1-0-1-0; metatarsus d0-1-2, v2-2-1, p1-1-1, r1-1-1; tarsus 0; IV: femur d1-1-0-2, p0-1-0-1; patella 0; tibia v1-1-2, p1-1-1-0, r1-1-1-0; metatarsus d1-2-2, v2-2-1, p1-1-1, r0-0-1; tarsus 0. Epigynum (Figs. 16, 17): fossa divided by a moderately

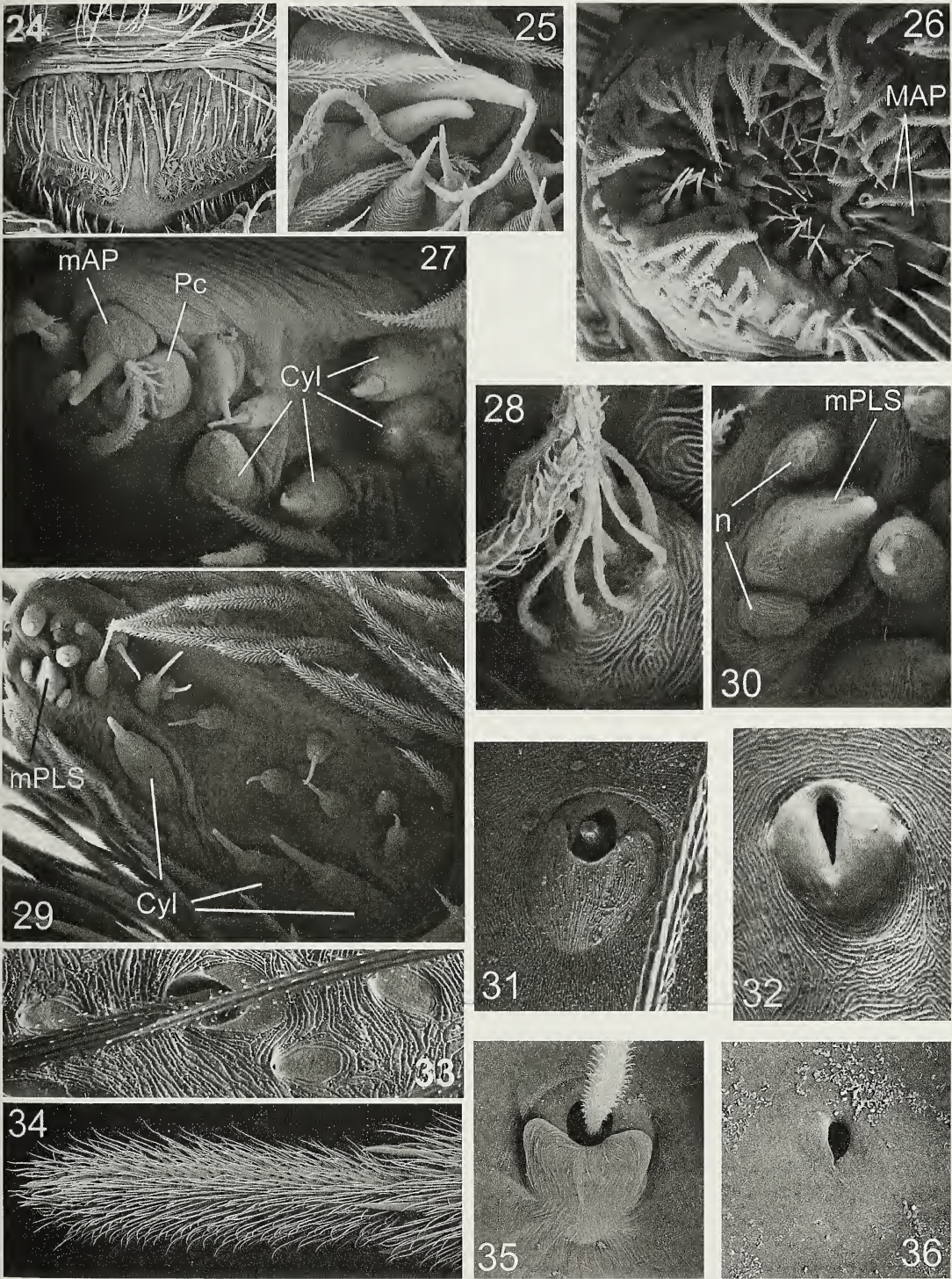
wide and arched median septum, becoming wider and lobe-like posteriorly; copulatory duct openings postero-lateral, ducts very short and narrow, entering the spermathecae antero-medially; spermathecae ovoid, well separated. Spinning organs (Figs. 18–23): cribellar plate bipartite, each field about a quarter as wide as long and separated by a narrow seam (about  $0.1 \times$  of a field length); seam and posterior plate margin sclerotized (in male, cribellum almost as wide as in female but with non-functional fields). Spinnerets short, ALS = PLS, PMS shortest; ALS broad, very short apical segment with wide margins; PLS slender with longer, conical apical segment. Spigots: ALS: 2 MAP spigots, mesal, adjacent, unequal; ca. 100 piriform spigots; PMS: 1 MAP with 4 fused paracribellar bases antero-ectally adjacent [5, 5, 2, 2 spigots respectively (2, 2 spigots basally fused only)]; 6 aciniform spigots (1 anterior, rest distributed); 6 cylindrical spigots; PLS: ca. 16 aciniform spigots, distributed; 1 subapical “modified PLS” spigot with 1 paracribellar spigot, and 1 nubbin almost entirely fused to side of mPLS; 7–8 cylindrical spigots (basal to subapical).

**Variation.**—Given the distribution of this species across dissected highland forest terrain, it is not surprising that considerable morphological variation is encountered. In females, the epigynal septum may be moderately wide (Fig. 16) or much narrower. The loops of the sperm duct on the tegulum may be open or closed and vary in size. The MA is usually large and obvious but its size and shape vary (Figs. 11, 13); some reduction is evident in a male specimen from the Mt Buller region (Fig. 14), but the specimen is badly damaged and more material is needed to check its specific status.

**Distribution.**—Central Highlands of Victoria (Southern Great Dividing Range) from the Mt Buller region to Warburton and west to the Macedon region.

**Biology.**—Cribellate sheet webs associated with logs, rocks and soil banks, guyed out with coarse retreat threads; sheet tapers to a variably defined retreat funnel ending inside a log or rock cavity or in a shallow soil burrow. Spiders run underneath sheet. Two egg sacs made of fine white flocculent silk (AM KS45401 and KS45403) were observed at Mt Macedon in February 1996. They were both found within cavities in rotting logs near the





Figures 24–36.—*Taurongia* species: 24–30. *T. ambigua* new species, spinnerets (female). 24. Cribellum; 25. MAP spigots, ALS (RHS); 26. ALS (LHS); 27. PMS (LHS); 28. Paracribellar spigots, PMS; 29. PLS (LHS); 30. mPLS spigot and nubbins (n) on apical PLS. 31–36. Sensilla (tarsus 1). 31–33, *T. ambigua* new species: 31. Trichobothrium base; 32. Tarsal organ; 33. Cuticular patterning and ovoid sensillae. 34–36, *T. punctata*. 34. ventral tarsal hairs; 35. Trichobothrium base; 36. Tarsal organ.



base of their respective retreat funnels. Each sac was ca. 1 cm in diameter, circular in plan, curved above but flatter below and suspended within a network of strong threads attached to the retreat walls.

***Taurongia ambigua* new species**

Figs. 5–7, 9, 10, 24–33, 37–41

**Type material.**—AUSTRALIA: *Victoria*: Holotype ♂, 12 km from Halls Gap on Victoria Valley Road, Grampians Range, 3708'S 142°31'E, under log in small, irregular sheet web, tall open forest, 26 March 1974, M.R. Gray (AM KS45501). Paratypes: 1 ♀, same data as holotype (AM KS5292); 3 ♀, same data as holotype except 27 March 1974 (AM KS5290, KS88171–72); 1 ♀, same data as KS5290 except web under rock in gully (AM KS45502).

**Other material.**—AUSTRALIA: *Victoria*: 1 ♀, same data as AM KS5290, abdomen used for SEM (AM KS88173).

**Etymology.**—A reference to the uncertain generic placement of this species.

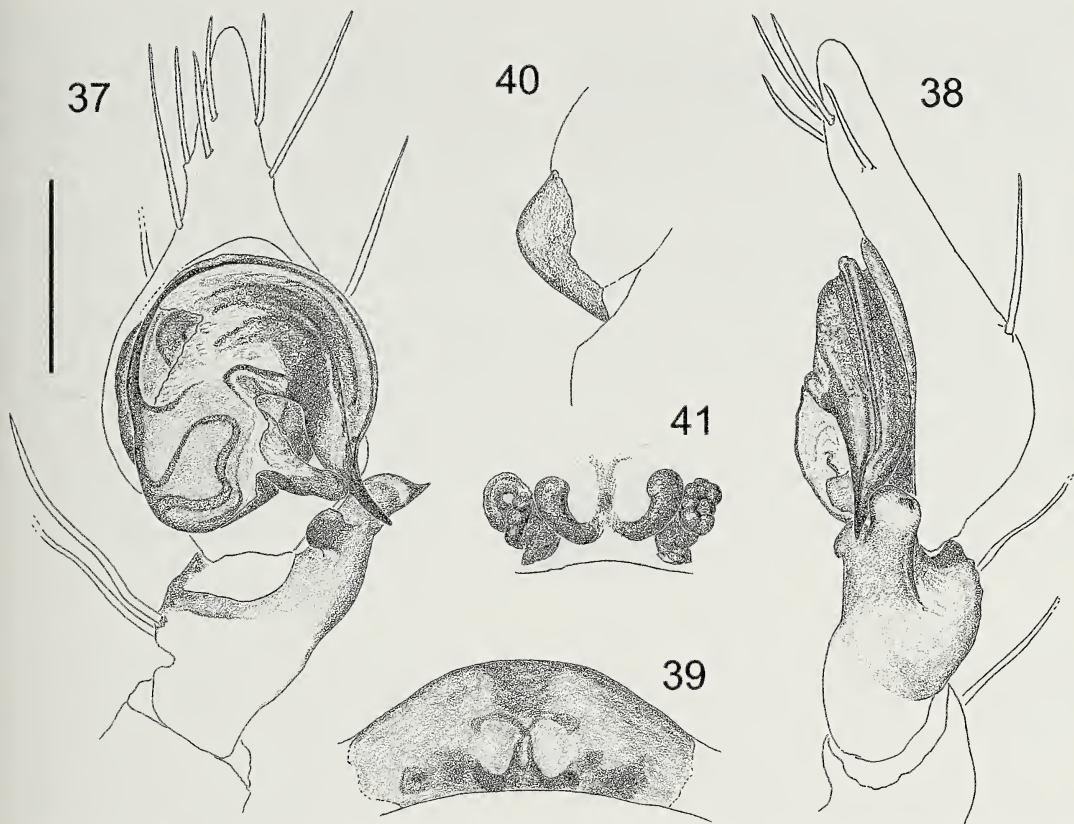
**Diagnosis.**—Differs from *T. punctata* by its gracile build (narrow caput, slender legs), relatively larger eyes with AME smallest, deeply notched trochanters, undivided epigynal fossa, elongate retrolateral conductor limb and strong cuticular sculpturing.

**Description.**—*Male (holotype)*: BL 6.77, CL 3.75, CW 2.65, CapW 1.45, EGW 0.88, LL 0.59, LW 0.54, SL 1.78, SW 1.56. Gracile cribellate spiders. Carapace amber-brown, darkest at caput; patterning restricted to radiating darker lines from fovea. Abdomen dark grey-brown with dark anterodorsal stripe flanked by 5 pallid patches smallest posteriorly, and 3 pairs of pallid lateral stripes (Fig. 7). Carapace weakly arched. EGW ca.  $0.6 \times$  width of caput. Eyes normal size (relatively larger than in *T. punctata*), AME smallest: ALE  $\geq$  PLE  $\geq$  PME  $>$  AME (Fig. 9). Jaws vertical, boss small. Sternum cordate, extending posteriorly between coxae 4. Legs: relatively long, slender, 1423 (I: 18.73; II: 14.55; III: 12.47; IV: 15.60); ratio tibia I length: CW =  $1:0.54$ . All trochanters deeply notched. Hairs plumose, most inclined, a few vertical; feathery hairs absent; metatarsi and tarsi not ventrally hirsute; 1<sup>st</sup> and 2<sup>nd</sup> metatarsi and tarsi with many long, curled hairs. Spination: I: femur d1-2-0-2, p0-1-1-1; patella 0; tibia v2-2-2, p1-1-0-1-0, r0-1-0-1-0; metatarsus d0-0-2,

v2-2-1, p0-1-0-1, r0-1-1; tarsus 0; II: femur d1-2-0-2, p0-1-1-1; patella 0; tibia d0-0-1-0, v2-2-2, p0-1-0-1-0, r0-1-0-1-0; metatarsus d2-2-2, v2-2-1, p0-0-1, r0-0-1; tarsus 0; III: femur d1-2-2, p0-1-1; patella d1-0-1; tibia d1-0-1-0, v2-2-2, p0-1-0-1-0, r0-1-0-1-0; metatarsus d2-0-2, v2-2-1, p0-1-0-1, r0-1-0-1; tarsus 0; IV: femur d1-1-2, p0-0-1; patella d0-0-1; tibia d1-0-0-1-0, v2-2-2, p0-1-0-1-0, r0-1-0-1-0; metatarsus d2-1-2, v2-2-1, p0-1-0-1, r0-0-1; tarsus 0. Male palp (Figs. 37, 38): conductor T-shaped with a slender, elongate retrodistal spine. TW present, larger than in *T. punctata*. Large 'spatulate' MA, membranous, partly hyaline. Large ventrad RTA with pointed apex, with a smaller, blunt RVTA arising at its base.

*Female (Grampians Range, AM KS5292)*: BL 7.35, CL 3.64 (range 2.85–3.68), CW 2.47, CapW 1.56, EGW 0.86, LL 0.61, LW 0.54, SL 1.82, SW 1.55. Legs lacking numerous curled hairs of male and ventral metatarsi III, IV more hirsute distally. Otherwise body, eyes and legs similar to male. Legs: 1423 (I: 13.71; II: 11.56; III: 10.55; IV: 12.80); ratio tibia I length: CW =  $1:0.71$ . Tarsal claws: superior, 5–7, inferior, 0–2; with 2–3 curved sustentacular hairs. Cuticle strongly sculpted with a closely ridged surface pattern, interrupted by numerous ovoid, plaque-like putative sensilla with small distal pores (Fig. 33). TO capsule finely ridged with a narrow, ovoid, keyhole-like pore (Fig. 32). Spination: I: femur d1-2-2, p0-1-1-1; patella 0; tibia v2-2-2, p1-1-0-1-0, r0-1-0-1-0; metatarsus d0-0-2, v2-2-1, p0-1-0-1, r0-1-0-1; tarsus 0; II: femur d1-2-1-2, p0-1-1-1; patella 0; tibia v2-2-2, p0-1-0-1-0, r0-1-0-1-0; metatarsus d0-0-2, v2-2-1, p1-1-0-1, r0-1-0-1; tarsus 0; III: femur d1-2-0-2, p0-1-1-1; patella d0-0-1; tibia d1-0-1-0, v2-2-2, p0-1-0-1-0, r0-1-0-1-0; metatarsus d2-1-2, v2-2-1, p0-1-0-1, r0-1-0-1; tarsus 0; IV: femur d1-0-1-0-2, p0-1-0-1; patella 0; tibia d1-0-0-1-0, v2-2-2, p0-1-0-1-0, r0-1-0-1-0; metatarsus d2-1-2, v2-2-1, p0-1-0-1, r0-0-1; tarsus 0. Calamistrum short, less than  $0.25 \times$  length of metatarsus, in 2<sup>nd</sup> proximal quarter of metatarsus IV. Epigynum (Figs. 39–41): epigynal fossa open, without a distinct septum but with a median seam or low ridge. Copulatory duct openings postero-lateral, ducts longer and wider than in *T. punctata* and curved around spermathecae. Spinning organs: (Figs. 24–30). PLS very slender





Figures 37–41.—*Taurongia ambigua* new species: 37, 38. Male palp, ventral and retrolateral; 39, 40, 41. Epigynum, ventral, lateral and dorsal. Scale bar: 0.25 mm.

and shorter than ALS. Cribellar plate bipartite, each field about a third as wide as long and separated by a wide seam (about  $0.3 \times$  a field length); Spigots: ALS: 2 MAP spigots, mesal, adjacent, unequal; 50–60 piriform spigots; PMS: 1 mAP; 1 fused paracribellar base (5–7 spigots); 4 aciniform spigots (1 anterior); 4 cylindrical spigots; PLS: 12 aciniform spigots, distributed; 1 subapical “modified PLS” spigot; paracribellar spigots absent but at least 2 nubbins present flanking mPLS; 3 cylindrical spigots.

**Distribution.**—Recorded only from the type locality.

#### RELATIONSHIPS OF *TAURONGIA*

An analysis of the relationships of amaurobioid spiders with grate-shaped eye tapeta [exemplified by the genera *Borrada* Gray & Smith 2004 and *Pillara* Gray & Smith 2004 (Gray & Smith 2004)] suggests that *Taurongia* lies at the base of a group of genera including *Stiphidion* Simon 1902 and *Wabua*

Davies 2000, which in turn is basal to the “grate-shaped tapetum” genera. This data (in preparation) suggests that *Taurongia* may be associated with the Stiphidiioidea of Griswold et al. (1999).

#### ACKNOWLEDGMENTS

I am grateful to Peter Lilywhite (Museum of Victoria) and Mark Harvey (Western Australian Museum) for the loan of material from their respective collections. Paul Hillyard (Natural History Museum) kindly provided me with access to the type material of *Taurongia*. The genitalic illustrations were made by Helen Smith.

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## REVISION OF SPIDER TAXA DESCRIBED BY KYUKICHI KISHIDA: PART 1. PERSONAL HISTORY AND A LIST OF HIS WORKS ON SPIDERS

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**ABSTRACT.** The personal history of forgotten Japanese arachnologist, Kyukichi Kishida (1888–1968) is described for the first time based on information collected from the literature and through interviews with the late Prof. Seikichi Kishida (1931–2002), the fourth son of K. Kishida. A complete list of Kishida's works on spiders is provided. Much confusion resulted from the species and higher taxa descriptions or species designations made by Kishida. In many cases he first proposed a new name for an undescribed species found but left its description to his followers. Therefore, some species were really described by another person, while many *nomina nuda* were produced. A revision of each taxon with systematical and nomenclatural problems will be given in forthcoming parts of this serial (in preparation).

**Keywords:** Bibliography, arachnology, Kyukichi Kishida, Japan

Kyukichi Kishida (1888–1968) was a Japanese zoologist who studied morphology and systematics of various groups of animals including spiders, mites, pseudoscorpions and other arachnids, myriapods and insects, as well as sipunculids, birds and mammals. He described from Japan not only small animals such as spiders, mites and beetles, but also some mammals such as a bat, a vole and even a wolf.

He was a pioneer in the history of Japanese arachnology. Because nobody presented lectures on arachnology in Japanese universities at that time, he taught himself with European literature and founded some zoological societies in Japan. His students included: Seiji Yuhara (1906–1929), Toshio Uyemura (1909–1988), Makoto Yoshikura (1911–2003), Koji Nakatsuji (1911–1945), Toshihiro Komatsu (1911–1982), Izumi Kayashima (1911–), Yasunosuke Chikuni (1911–2005), and Takeo Yaginuma (1916–1995). Most present-day Japanese arachnologists including the present author were influenced intellectually by T. Yaginuma who made an effort to popularize arachnology in Japan with his book, 'Spiders of Japan in Colour' (Yaginuma 1960).

In 1929, Kishida established Lanzan-kai, The Society of Arachnology and Zoology, in Tokyo and published the journal, *Lansania* (Fig. 1). The figure on its cover indicates Lanzan Ono (1729–1810) to whom Kishida paid

respect. Lanzan Ono was an active herbalist in the Edo Era (1603–1867), who published a series of books on Japanese flora and fauna. The society of Lanzan-kai was, however, not always successful and became inactive after only a few years. The Arachnological Society of East Asia was established in 1936 under Kishida and took the place of the Lanzan-kai, and the organ *Acta Arachnologica* has been continuously published for about 70 years.

Despite these accomplishments, Kishida's legacy is poorly known and some of his spider taxonomy has created considerable confusion. For instance, of more than 100 publications by K. Kishida (see the following pages), only four are listed in Roewer (1942), three in Bonnet (1945), 24 in Brignoli (1983), and only a few are included in the newest international database (Platnick 2005). His works were forgotten even by Japanese arachnologists.

Many of the taxa named by Kishida were not always described correctly and the depository of his collection was unknown. Consequently, these were left as *nomina nuda*. Only a few cases have been solved, for instance, *Prodidomus imaidzumii* Kishida 1914 was re-described by Platnick (1976), the salticid *Chirothecia insulana* Kishida 1914 was revised and transferred to *Harmochirus* by Logunov et al. (1997), the corinnid genus *Utivarachna* Kishida 1940 was recognized by Deeleman-Reinhold (2001), and a small theraphosid

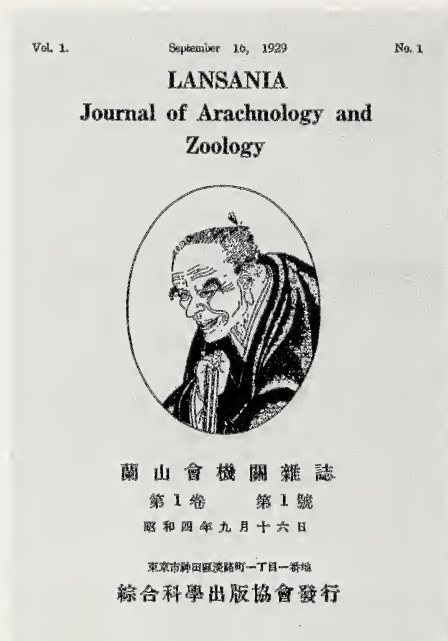


Figure 1.—Front cover of *Lansania*, the first arachnological journal in the world (commenced in 1929) published by Kyukichi Kishida.

from Taiwan, *Yamia watasei* Kishida 1920 was recently redescribed by Haupt & Schmidt (2004).

The purpose of this study is to bring the whole aspect on problematical names of spiders caused by Kishida's treatment to light by providing: 1) his personal history and a character sketch, 2) a list of his publications on spiders, 3) a list of spider taxa named by him, 4) a list of valid names extracted from these, 5) a list of *nomina nuda*, and 6) information on type specimens. This contribution deals with parts 1 and 2. The remaining sections will be provided in forthcoming publications.

#### METHODS

Information about Kishida's personal history was acquired through interviews with the late Prof. Seikichi Kishida (1931–2002), the fourth son of Kishida. Publications by Kyukichi Kishida were found by searching the library complexes of universities in Japan, and a complete list of his works was made. The missing depositories of his spider collection were followed up. All the Latin names of spiders made by K. Kishida were listed from his papers as well as those of other Japanese arachnologists and their originality and author-

ship were determined according to the past and present rules of the International Code of Zoological Nomenclature. The systematic position of species with valid names was judged based on comparison with specimens in the arachnid collection of the Department of Zoology, National Science Museum in Tokyo. Some new synonymies are determined. Valid names as well as remaining *nomina nuda* are herein listed.

#### RESULTS

**Brief Personal History of Kyukichi Kishida.**—Kyukichi Kishida was born in 1888 at Maizuru in Kyoto Prefecture, in central Japan. He grew up during the middle of the Meiji Era (1868–1912), during which Japan became very quickly westernized. Between 1603 and 1867 (Edo Era) this country was closed and isolated from European sciences. Since Ludwig Koch (1878) first reported on Japanese spiders with Latin names, only European people led this field. Bösenberg & Strand (1906) described about 400 species and recorded almost all the common species in the Japanese spider fauna.

After graduating from the Teachers' College of Kyoto Prefecture in 1908, Kishida began his career as a teacher in a primary school. At the same time he learned zoology from the European literature and published his first report (1907) on a spider. This paper was the first by a Japanese researcher to describe a spider species in Latin. Between 1913 and 1914, he published a monograph of Japanese spiders serially in 12 parts in the *Scientific World*.

In 1915, he moved to a junior high school in Odate, northern Japan, and gave lectures on biology, geology and even music. However, after three years he resigned and entered the Department of Zoology of Tokyo University to study zoology. In 1921, he was employed at the Ministry of Agriculture as a scientist. Some of his most important papers were written at that time, for instance on *Yamia* Kishida 1920 (Kishida 1920) and *Heptathela* Kishida 1923 (Kishida 1923). He always considered it more important to place species in a systematic context within the Araneae rather than to record and describe each species.

In 1940, he was employed at Waseda University as a lecturer but had to be evacuated from Tokyo in 1944 due to the situation cre-



ated in the city from the events of World War II. He moved to his home in Kyoto to escape the bombings by the American Air Force. After the war he returned to Tokyo in 1948 and was employed at the Forestry Agency. Unfortunately, the great confusion in social conditions that prevailed in Japan for about ten years during and after the war decreased his activities in arachnology and his interest tended mainly toward mammalogy and ornithology during this period.

Late in life in 1961, he received the Doctor of Science degree at Hiroshima University with a study in osteology of the Japanese Serow *Capricornulus* (an artiodactyle) and in the next year he received the Doctor of Agriculture at Tokyo University of Agriculture with a study of Lagomorpha.

He died at the age of 80 in 1968 from Parkinson's disease. Many unpublished manuscripts found at his home after death suggested that his erudition with extensive knowledge in zoology may not be shown in full. In 1969, the Arachnological Society of East Asia published Nos. 49/50 of *Atypus* as a memorial issue for K. Kishida. M. Yoshikura, T. Komatsu, I. Kayashima, K. Morikawa, T. Yaginuma and T. Uyemura wrote memoirs of him.

It is both a strong and a weak point of his character that he had such a wide range of knowledge and interests in zoology. At the time, he was the only specialist in Japan who knew the names of spiders. This led him to assign a new name first without providing a formal description, particularly when he obtained undescribed species collected during zoological expeditions and was asked to identify the specimens. The formal descriptions he left to his followers and sometimes he returned the specimens to the collectors. It depended on his followers whether this new species would be really described or only cited with Latin names probably assigned by Kishida. Therefore, many *nomina nuda* exist, while some were described by other researchers. For example, an araneid, *Suzumia orientalis* named by Kishida was described three times by Yuhara (1931), Nakatsudi (1943) and Kayashima (1943) from different type localities in Japan and Taiwan. Although the species was regarded as a junior synonym of *Cyrtophora moluccensis* (Dolleschall 1857) *sensu lato*, the authorship needs to be confirmed for the future phylogenetic analysis on this group



Figure 2.—Portrait of Kyukichi Kishida in 1964. [Photograph by Seikichi Kishida.]

(Ono 1994). Explanation of each systematic and nomenclatural problem will be given in the coming parts of this subject (in preparation).

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## FORAGING STRATEGIES OF *ERIOPHORA EDAX* (ARANEAE, ARANEIDAE): A NOCTURNAL ORB-WEAVING SPIDER

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**ABSTRACT.** Studies on the ecology of orb spiders have focused on diurnal spiders, especially field studies. Nocturnal spiders, however, face different conditions due to the type of prey found at night. A field study was conducted to observe the activity of adult females of *Eriophora edax* in their natural environment, and to analyze their predation efficiency and web retention properties. Most of the spiders were observed around sunset, which suggests that *E. edax* tends to build webs in the early evening. In order to evaluate the predation efficiency of *E. edax* we compared its behavior and web retention properties with the behavior of a diurnal orb-weaving spider, *Verrucosa arenata*. Two prey types, a diurnal Hymenoptera and a nocturnal Lepidoptera, were selected and presented to the spiders, to record approach time and prey capture time. The results showed that *E. edax* spent more time to capture Hymenoptera than to capture Lepidoptera. During the experiments of web prey retention time, Hymenoptera consistently showed greater tumbling than Lepidoptera, but the total retention time was the same for both prey types. Our results showed that *E. edax* forages strictly at night and, in terms of prey capture and web retention, was more efficient when preying on Lepidoptera.

**Keywords:** *Eriophora edax*, web-building spider, nocturnal activity, prey selection.

Web-building spiders present a unique case of “sit-and-wait” predation (Heiling 1999), so they are not expected to exhibit prey specialization (Uetz 1990). However, recent studies have shown that many web-building spiders exhibit considerable dietary specialization (Riechert & Luczak 1982; Stowe 1986; Nentwig 1987). For example, *Tetragnatha montana* Simon 1874, an orb weaver found in Eastern Europe, feeds mainly on mosquitoes (Dabrowska-Port & Luczak 1968; Dabrowska-Port et al. 1968; Luczak 1980). Habitat choice and activity pattern of the species are closely tied to the occurrence and activity of the preferred prey (Uetz 1990).

It has been suggested that nocturnal web-building, particularly in the tropics, is an adaptation to avoid the visibility of webs in daytime (Rypstra 1979, 1982). The optical properties of some orb webs tend to reduce its visibility, especially in low-light and varying

background conditions (Craig et al. 1985; Craig 1986). Several species of orb weaving spiders ingest their previous web and replace it with a new one (Breed et al. 1964; Eberhard 1971; Carico 1986). The renewal of the web is critical, because a web’s ability to capture food decreases over time as a result of contact with prey and non-prey items that destroy both threads and glue (Chacon & Eberhard 1980).

In a study on the predatory capacity of four sympatric species of web-building spiders that inhabit coffee plantations in Southern Mexico, Hénaut et al. (2001) found that the consumption of prey was related to the predatory strategy of each spider species. For example, *Gasteracantha cancelliformis* (Linnaeus 1785), a diurnal orb weaving spider, built a new web every morning and prey storage was never observed. In contrast, *Cyclosa caroli* (Hentz 1850), another diurnal orb web spider, built a “permanent” web (only renewed when damaged) and stored prey on a stablimentum,

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which may explain the very low incidence of immediate prey consumption observed in this species (Hénaut et al. 2001). However, a census of the prey captured by *C. caroli* and *G. canciformis* showed that both species have a marked positive electivity for Diptera and Hymenoptera (Ibarra-Núñez et al. 2001).

There are numerous reports concerning predation by web-building spiders (Heiling 1999; Hénaut et al. 2001; Ibarra-Núñez et al. 2001) although the vast majority involves diurnal species. In contrast, the present study investigated the foraging activity of a nocturnal orb web spider, *Eriophora edax* (Blackwell 1896 (Araneidae)). This Pan-american species with a body length ranging from 12–16 mm (Levi 1970) was selected due to its nocturnal activity and its abundance. The web of *E. edax* is vertical, and the spider stays at the hub of the web with its head facing down.

The study was divided in two parts. First, we examined *in situ* the activity and the prey captured by adult females of *E. edax*. Second, we compared the prey capture behavior of *E. edax* with the prey capture behavior of a diurnal orb weaving spider.

## METHODS

**Study site.**—The study was conducted in July and August 2002 in a coffee plantation at the agricultural experimental station “Rosario Izapa” of the INIFAP (Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias), situated at 400 m above sea level in the state of Chiapas, southern Mexico (14° 58' N, 92° 09' W). The climate is tropical, warm and humid. Heavy rainfall (3000 mm per month) occurs from May–October. During the course of the study, temperature fell to approximately 23 °C at night, and rose to about 33 °C during the day. The relative humidity was around 85%, day and night.

**Spider activity.**—We observed the spiders' activity for three nights without rain (when spiders are active and observers can stay the entire night in the field). Observations were done from 1800 to 0700. At this time of the year sunset occurred between 1900 and 1930 and sunrise between 0630 and 0700. We walked hourly along a 200 m transect (using a chronometer to check the time), to check for *E. edax* spiders and their webs. It took from 30–45 min to record all the spiders of a transect. Flashlights with dark red plastic cover

facilitated observation while neither attracting insect prey, nor disturbing the spiders' natural photoperiod (Herberstein & Elgar 1994; Heiling 1999).

On each transect walk we recorded the spiders present in the bush with or without a web and the absence of individuals previously recorded. We marked spiders' positions individually with a numbered piece of white plastic located on the nearest twig. Spider activities were recorded as: building the web, catching a prey (when a spider was wrapping a prey with silk), and eating a prey (when a spider was actually biting a prey or was handling it in its chelicerae).

All voucher specimens are deposited in the Collection of the Laboratory of Arthropod Ecoethology (Laboratorio de Ecoetología de Artrópodos) in Ecosur, Tapachula, Mexico.

**Spiders' prey.**—Prey items captured in the webs were visually identified to the level of order. These prey items were not removed from the webs. Prey identification to lower levels, although desirable, would have resulted in substantial disturbance of the webs. We compared the hourly numbers of each order of prey captured by *E. edax* web with a Chi-square test (SPSS 10.00 for Windows).

**Predation efficiency and web retention properties.**—In order to evaluate the predation efficiency and the web retention properties of *E. edax*, we conducted two field experiments during the same months but on different nights than the activity observations. We selected *Verrucosa arenata* (Walckenaer, 1841) (body length: 8–15 mm) as a model of diurnal orb weaving spiders. Like *E. edax*, it is an araneid, builds its web every day, and dismantles it at the end of its daily activity period. However, it is as strictly diurnal as *E. edax* is nocturnal. Finally, *V. arenata* is present in the same habitats as *E. edax*. Two experimental prey types were selected, because they are abundant in the coffee plantation (Ibarra-Núñez 1990). Adults of the moth *Sitotroga cerealella* (Olivier 1819) (Lepidoptera, Gelechiidae) were selected as representatives of a nocturnal prey, while the stingless bee *Scaptotrigona mexicana* Guérin (Hymenoptera, Apidae) was chosen as an example of a diurnal prey. Prey specimens were obtained from laboratory cultures. For both prey types, field experiments were performed during three days for *V. arenata* and during three nights



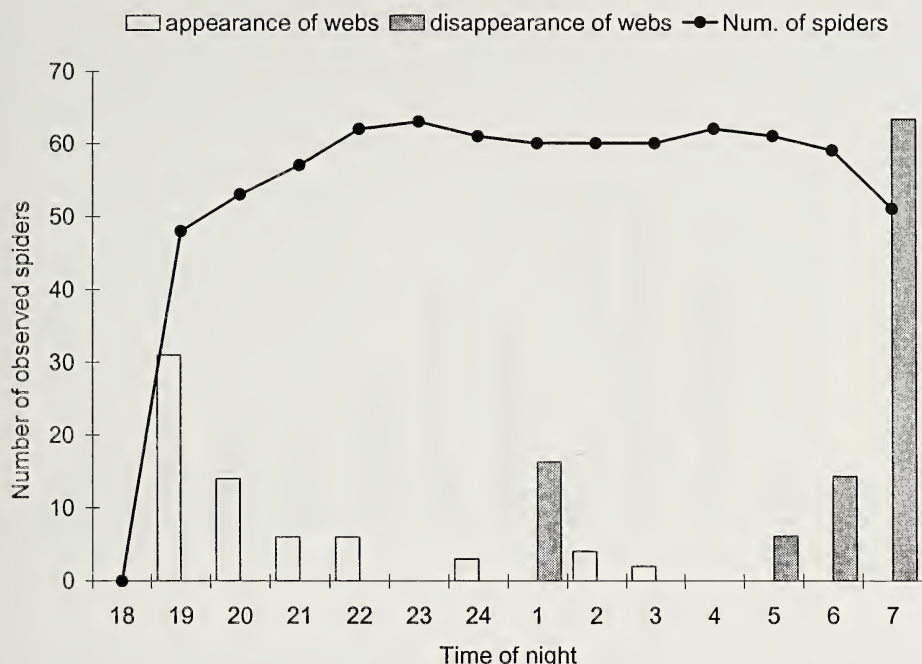


Figure 1.—Number of *Eriophora edax* individuals with or without a web (number of spiders), appearance of webs and disappearance of webs in the study site during a 12 hour observation period. Sunset occurred between 1900 hrs and 1930 hrs; sunrise between 0630 hrs and 0700 hrs.

for *E. edax*. For each type of prey and for each spider species, 20 individuals were tested for the predation and web retention studies. For each prey type, observations were made in the same 24 hour period for both spider species.

For the predation efficiency experiments, webs were selected based on the following criteria: no signs of remains of prey, spider was an adult female located at the center of the web. Each prey item was gently blown into the web with the aid of an inverted aspirator from a distance of 10 cm. All prey were alive and visually undamaged before and after introduction into the web.

Once the prey made contact with the web, the behavior of the spider was registered in terms of approach and prey capture (measured in seconds). The prey capture event started at the moment the spider bit the prey, continued with its manipulation and finished when the spider took it to the center of the web. Observations were conducted for a 5 min period, which was enough for recording the complete capture event. We compared the predation efficiency of both spider species with both types of prey with an ANOVA (Statistica 6.0).

For the web retention experiments, webs

were selected based on the same criteria as above. Spiders were carefully removed from their web, and prey items were blown the same way as mentioned before. Once the prey made contact with the web, a small piece of paper was set at the impact point to measure the distance the prey tumbled. The prey was observed for a 5 min period, after which the tumbling distance was measured in centimeters. If the prey remained on the web for more than 5 min, a second tumbling distance of the same prey was measured after 30 min. Once the experiment ended, the spider was returned to its web. The data obtained from both observation periods (5 min and 30 min) were contrasted for spider and prey types (nocturnal vs. diurnal) with an ANOVA (Statistica 6.0).

## RESULTS

**Spider activity.**—*E. edax* was not observed before 1900. Most of the spiders appeared on coffee bushes or were building their webs between 1900–1930, around sunset time ( $n = 48$  of a total of 74 spiders observed for the three nights). Around 68% of the spiders were present between 1900 and 2000, and we

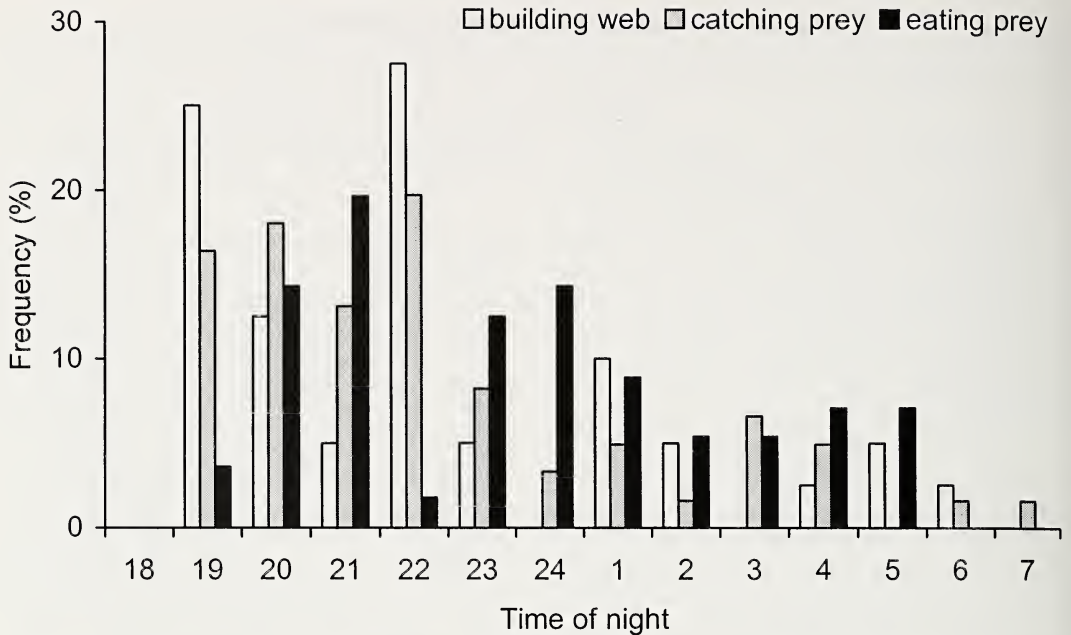


Figure 2.—Frequency of web building, prey catching and prey eating by *Eriophora edax* in a coffee plantation during the 12 hrs observation period. Sunset occurred between 1900 hrs and 1930 hrs; sunrise between 0630 hrs and 0700 hrs.

observed no spider after 0700, when the sun rose (Fig. 1).

Although spiders were able to build their web all night, this activity was more intense between 1900 and 2200. Other smaller peaks of this activity occurred around 0100 and 0500. *E. edax* requires less than one hour to build its web, as the web was completed between two subsequent data recordings, and most often the spiders had already caught a prey when its web was observed for the first time (Fig. 2).

Catching prey was most intense at the beginning of the night, between 1900 and 2300. Then the catching activity decreased through the night, although this activity increased again slightly between 0300 and 0400 just after the second peak of building (Fig. 2).

Spiders began to eat prey at 1900, but this activity peaked at 2100, right after the peak of catching activity. Other smaller peaks of eating activity occurred at 0000, and between 0400 and 0500. We also observed that spiders stopped eating before sunrise (0700), even if they had caught a prey (Fig. 2).

*E. edax* is more active at the beginning of the night than at the end of the night (Fig. 2).

Of the 74 spiders observed during the three nights, 55.4% caught only one prey, 9.5% caught two prey and 35.1% did not capture any prey.

**Spiders' prey.**—The main prey items caught by *E. edax* ( $n = 55$ ) were Lepidoptera (67.7%), Coleoptera (21.5%), Diptera (9.2%), and Hymenoptera (1.5%). Minor taxa included Orthoptera and Hemiptera ( $< 0.1\%$ ). The number of prey items of different insect orders differed statistically ( $\chi^2 = 150.7$ , d.f. = 8,  $P = 0.001$ ). Lepidoptera were mostly caught at the beginning of the night (1900–2100) with a second, smaller peak of capture between 0300 and 0400. Coleoptera were caught by the spiders between 1900 and 2200.

**Predation efficiency and web retention properties.**—The time spent to reach and capture a prey as well as the tumbling of the prey into the webs varied according to the spider species (Table 1). *E. edax* spent less time to reach Lepidopterans but more time to capture Hymenopterans than *V. arenata* and the tumbling is more important with the web of *E. edax* (Table 1). However, the comparison between prey show that the time spent to reach



Table 1.—Time (in seconds  $\pm$  SE) of each spider species (*Eriophora edax* and *Verrucosa arenata*) to reach and to capture the offered prey (Lepidoptera and Hymenoptera), as well as each prey's tumbling distance (in cm) in the web after 5 min and after 30 min of observation. \*\*\*,  $P < 0.001$ ; \*,  $P < 0.05$ ; ns, Not significant  $P > 0.05$ , ANOVA.

		<i>E. edax</i>	<i>V. arenata</i>	Comparison
Time to reach prey (sec)	Lep.	3.3 $\pm$ 0.7	46.3 $\pm$ 18.3	*
	Hym.	12.8 $\pm$ 8.6	17.2 $\pm$ 7.5	ns
Prey capture time (sec)	Lep.	18.1 $\pm$ 1.9	20.6 $\pm$ 5.2	ns
	Hym.	71.3 $\pm$ 7.5	20.7 $\pm$ 2.6	***
Tumbling after 5 min (cm)	Lep.	1.1 $\pm$ 0.8	1.9 $\pm$ 1	ns
	Hym.	5.2 $\pm$ 1.02	4.8 $\pm$ 1.3	ns
Tumbling after 30 min (cm)	Lep.	8.6 $\pm$ 1.2	0.8 $\pm$ 0.4	***
	Hym.	8.5 $\pm$ 1.2	5.8 $\pm$ 1.6	ns

a prey was not significantly different between the two prey types ( $F_{1,38} = 2$ ;  $P = 0.16$ ).

We also found significant differences in the prey capture time between the two spider species. *E. edax* spent more time to capture Hymenoptera than to capture Lepidoptera ( $F_{1,38} = 46$ ;  $P = 0.000$ ). On the other hand, the time *V. arenata* spent to capture both Hymenoptera and Lepidoptera did not differ significantly ( $F_{1,38} = 0.000$ ;  $P = 0.9$ ).

Prey tumbled differently according their type (diurnal or nocturnal), and to the spider species to which the web belonged, for both observation periods (5 min and 30 min). During the 5 min observation period, Hymenoptera tumbled a longer distance than Lepidoptera in *E. edax* and it tended to be the same in *V. arenata* webs (*E. edax*:  $F_{1,38} = 10$ ;  $P = 0.002$ ; *V. arenata*:  $F_{1,38} = 3.2$ ;  $P = 0.08$ ). During the 30 min observation period Hymenoptera tumbled a longer distance than Lepidoptera in *V. arenata* but the tumbling was not different in *E. edax* (*E. edax*:  $F_{1,38} = 0.005$ ;  $P = 0.9$ ; *V. arenata*:  $F_{1,38} = 15.6$ ;  $P = 0.000$ ).

During the 5 min observation period, both *E. edax* and *V. arenata* webs retained 100% of the blown prey. After 30 min, *E. edax* web retained 95% of the Lepidoptera and 90% of the Hymenoptera, and *V. arenata* webs retained 80% of Lepidoptera and 50% of Hymenoptera ( $\chi^2 = 0.5$ , d.f. = 1,  $P = 0.5$ ).

## DISCUSSION

Our results confirm that *Eriophora edax* forages strictly at night, spins a new web every night and dismantles it at dawn. Most spiders started to build their web just after sunset, and all spiders had disappeared at sunrise. Even if *E. edax* caught prey during the 12 h

observation period, it seems to have a strategy to "build, catch and eat" in a short period of time. Most prey is caught and eaten within a two hour period after the web is built. In comparison with other orb-weaving spiders (Hénaut et al. 2001) this spider captures a low number of prey (generally just one per night) and never makes prey caches. We did not observe *E. edax* relocate its web after capture and consumption of a prey. Thus, whether new arrivals during the night are new spiders or spiders building a second web in a new place, remains to be tested.

Capture rates were higher at the beginning of the night, probably due to the level of prey activity at this time (unpubl. data). As other *Eriophora* species, *E. edax* preyed mainly on Lepidoptera. For example, Herberstein & Elgar (1994) found that *E. transmarina* (Keyserling 1865) captured mostly Lepidoptera, which were also more abundant at night.

Another evidence of the strategy of *E. edax* to maximize capture time is that most spiders waited on their web almost all night, even when they had already caught some prey. Also, spiders did not dismantle their web until just before dawn, even if they had not caught or eaten a prey.

Although *E. edax*'s main prey was Lepidoptera it did vary its diet by eating other orders of insects, such as Coleoptera, Diptera, Hymenoptera, Orthoptera and Hemiptera. Nyffeler (1999) found that overall fewer than 10 arthropod orders (Diptera, Homoptera, Hymenoptera, Heteroptera, Collembola, Coleoptera, Lepidoptera, and Araneae) make up the bulk of the prey of common agroecosystem spiders. Dietary mixing seems to be advanta-

geous by optimizing a balanced nutrient composition needed for survival and reproduction (Greenstone 1979; Uetz et al. 1992; Toft 1995). However, in comparison with the diurnal spider *E. edax* is more efficient at reaching and capturing the moth than the bee, and its web offers a better prey retention for Lepidoptera than *V. arenata*'s web. The predatory behavior of the nocturnal spider seems to be more specialized towards moths, though the results on web retention might be influenced by differences in web properties caused by the difference in temperature between day and night (around 10 °C).

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## THE WASP SPIDER *ARGIOPE BRUENNICHI* (ARACHNIDA, ARANEIDAE): BALLOONING IS NOT AN OBLIGATE LIFE HISTORY PHASE

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**ABSTRACT.** Aerial dispersal (“ballooning”) of *Argiope bruennichi* spiderlings has been claimed to be an obligate life history trait and a prerequisite for spinning prey-capture webs. If this were true, a ballooning phase would be essential for any laboratory rearing of *A. bruennichi* making rearing protocols particularly elaborate. We tested the significance of ballooning for second-instar spiderlings in the laboratory and showed that the ballooning behavior is not essential for building prey-capture orb webs. Our results also give no evidence for the hypothesis that recent natural selection has changed ballooning behavior in newly founded field populations.

**Keywords:** Araneae, ballooning experiment, laboratory rearing, web-building behavior.

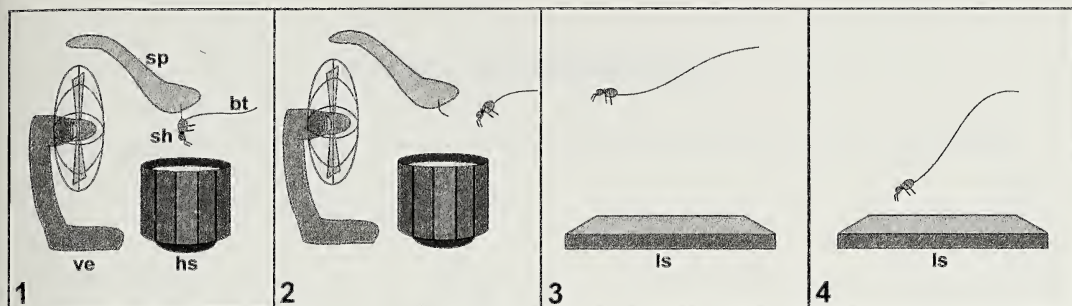
Ballooning is a common dispersal mechanism for many modern spiders (Coyle 1983; Dean & Sterling 1985; Weyman 1993), and this behavior is particularly important for maintaining genetic cohesion among *Argiope* populations (Ramirez & Haakonsen 1999). The life history of *Argiope* is characterized by ballooning, the aerial transport on wind-blown silk threads. A good example for the importance of ballooning for range expansion is the Palearctic wasp spider *Argiope bruennichi* (Scopoli 1772). The spider is an r-strategist (Guttmann 1979), characterized by high aerial dispersal capability and an ongoing postglacial expansion of its geographical range in Europe (van Helsdingen 1982). Females of *A. bruennichi* produce up to five cocoons in the field, often containing several hundred eggs (Crome & Crome 1961; Köhler & Schaller 1987). The expansion of the species has accelerated in the second half of the last century probably due to factors favoring dispersal by ballooning (Guttmann 1979; Levi 1983; Sacher & Bliss 1990; Scharff & Langemark 1997; Jonsson & Wilander 1999; Smithers 2000). The wasp spider prefers grassy or herbaceous vegetation in open, ephemeral or shrubby sites (Wiehle 1931; Pasquet 1984; Malt 1996) in coarse-grained (patchy) landscapes (Gillandt

& Martens 1980; Sacher & Bliss 1989) and has regionally benefited from an extension of farming production and urbanization (Lohmeyer & Pretscher 1979; Arnold 1986; Nyfeler & Benz 1987). River valleys have been identified as favored dispersal corridors further supporting the importance of ballooning for dispersion (Gauckler 1967; Puts 1988).

Follner & Klarenberg (1995) claimed ballooning to be an obligate phase in the development of *A. bruennichi*. These authors monitored the pre-ballooning and ballooning behavior of spiderlings in a grassland study site near Munich (Germany). Since they never found aggregations of orb webs in the neighborhood of the cocoons from which the overwintering second instar spiderlings eclosed and they only observed the construction of first prey-capture orb webs after a ballooning trip, they concluded “that aeronautic behaviour in Bavarian populations of *A. bruennichi* is obligatory”. Moreover, these authors suggested that spiderlings, which have hatched from the cocoon, will starve to death, unless they perform a ballooning trip. Ballooning should thus be an obligate phase to switch from a non-predatory, passive phase to one of active predation by spinning prey-capture orbs. Follner & Klarenberg (1995) argued that the obligatory aerial dispersal might be a result of recent natural selection and be the rea-

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Figures 1–4.—Design and course of the ballooning experiment. The spiderlings were placed on a spatula (sp) and exposed to a light air current by a fan (ve) and heat source (hs), which were placed at the left edge of a lab bench (240 cm). After cutting the drag line the spiderlings became airborne to land on the lab bench, which served as a landing strip (ls). 1. Pre-ballooning behavior: sp = spatula; ve = ventilator (light breeze); hs = heat source (25 Watt lamp, distance to spatula = 20 cm); sh = spiderling hanging from a dragline; bt = ballooning thread. 2. Initial ballooning phase. 3. Airborne spiderling: ls = “landing strip” (lab bench of 240 cm length). 4. Landing phase.

son behind the swift expansion of the species. New populations which are established during a period of expansion are always founded by individuals, which have ballooned.

If ballooning were a truly obligate phase, it would not only be important for natural selection but also be important for any rearing protocol for *A. bruennichi*. Allowing for ballooning in a rearing procedure might easily render laboratory breeding unfeasible as it could prove to be too time-consuming and laborious. However, an obligate ballooning phase has never been observed before, neither in other *Argiope* nor in the generally well studied *A. bruennichi*. Tolbert (1976, 1977) studied ballooning behavioral elements of *A. trifasciata* (Forskål 1775) and *A. aurantia* Lucas 1833. He concluded from field and laboratory observations that “it is unnecessary for spiderlings of either *Argiope* species to engage in aerial dispersal before building an orb web” (Tolbert 1977), which is an obvious discrepancy to Follner’s and Klarenberg’s (1995) claims. We here test the significance of ballooning for the construction of the first prey-capture web in the laboratory by comparing spiderlings reared under two experimental conditions, one with and one without ballooning.

We collected cocoons of *A. bruennichi* ( $n = 6$ ) in dry and semi-dry grasslands northeast of Halle (Saale) in late April 2002 (Germany, 160 m a.s.l., 51°33′31″ N, 011°52′49″ E). They were maintained in the lab in indi-

vidual glass vials (9 cm diameter, 13 cm height, coated with fine gauze) at  $23 \pm 2^\circ\text{C}$  and mist-sprayed with water every two days to avoid desiccation. The vial bottom was covered with initially wet cellulose wadding (1 cm). Second-instar spiderlings hatched from the cocoons in early May.

One day after hatching we simulated individual ballooning for 60 spiderlings (10 from each cocoon) by exposing the spiderling on a spatula to an air stream generated by a heat source and a fan (see Figs. 1–4 for details of the experimental design). We observed behavioral elements in the pre-ballooning phase in detail and noticed its mode. When the spiderling became airborne, we tracked it and retrieved it at the “landing strip” (Figs. 3, 4). The ballooning experiment was repeated immediately (re-ballooning) for each individual to satisfy a possible “ballooning drive” (see Tolbert 1977). The spiderlings had to actively participate in this experiment by showing the entire sequence of pre-ballooning and ballooning behavior (Figs. 1–4).

Following the experiments, the “ballooners” were kept in the same unheated indoor room with windows admitting indirect natural light. They were housed in groups ( $n = 20$ ) in three gauze covered glass terraria (50 × 30 × 31 cm;  $25 \pm 3^\circ\text{C}$ ;  $65 \pm 10\%$  RH) and fed ad libitum 45–50 live *Drosophila melanogaster* once a day. Every two days we sprinkled the inside surfaces of the terraria with water. This prevented desiccation and allowed for

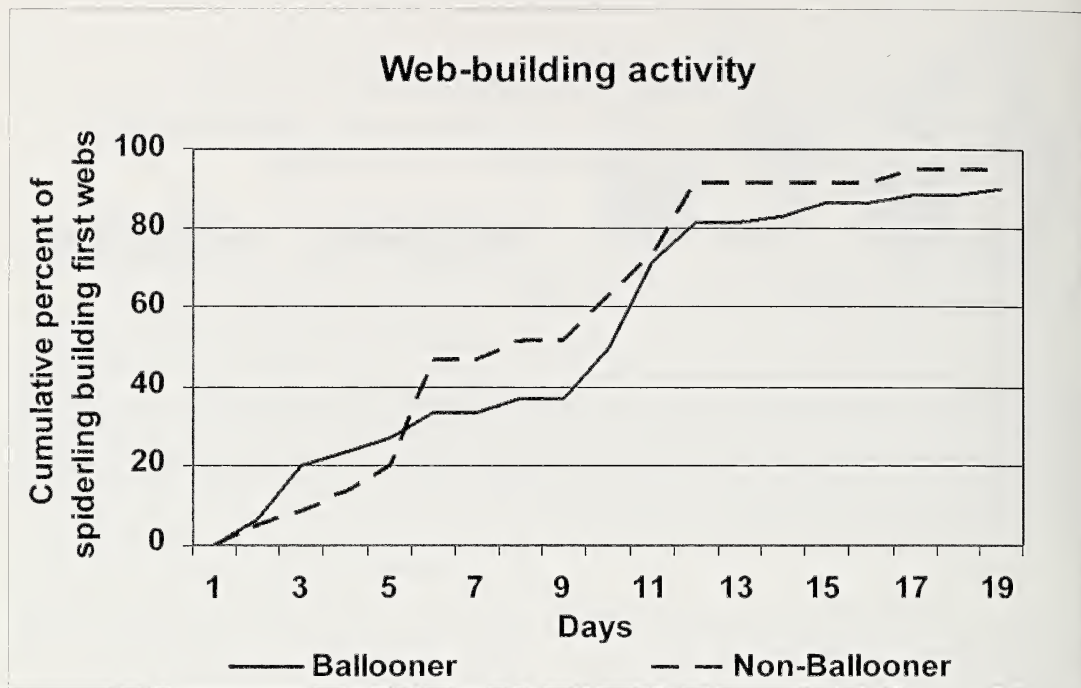


Figure 5.—Web-building activity of the *A. bruennichi* spiderlings during laboratory rearing for both ballooners and non-ballooners.

normal drinking behavior of the spiderlings. The bottoms of the terraria were covered with a layer of commercial, pasteurized potting soil (3 cm) with grass tufts, some dry twigs and wooden skewers to enhance the number of potential attachment points for web building.

A control group of spiderlings ( $n = 60$ ) was treated in the same way, but without the ballooning procedure ("non-ballooners"). In both groups (ballooners vs. non-ballooners) spiderlings and orb webs were noted three times daily at 6 a.m., 12 p.m. and 6 p.m. to ensure individual based data sets. The rearing period was cut off after 19 days when all the surviving individuals had spun their first prey-capture orb-webs.

Voucher specimens are deposited in the Entomological Collection of the Martin-Luther-University Halle-Wittenberg (Zoological Institute), Germany (identification number 2568).

The web-building activity of the spiderlings increased in both the ballooners and the non-ballooners over time and reached  $90 \pm 5\%$  for ballooners ( $n = 54$ , three terraria) and  $95 \pm 5\%$  for non-ballooners ( $n = 57$ , three terraria) within a period of 19d (Fig. 5). The differ-

ences in the web-building activity (Fig. 5) were not statistically significant between the two groups of spiderlings (Kruskal-Wallis test,  $P = 0.7515$ ; tested for daily built-first webs). The mean latency time for web-building (time from hatching from the cocoon to the construction of the first prey-capture web) was  $8.61 \pm 4.28$  days and  $8.18 \pm 3.60$  days for ballooners ( $n = 54$ ) and non-ballooners ( $n = 57$ ) respectively. This difference was not statistically significant (t-test,  $P = 0.56$ ).

Although mortality increased in the second half of the observation period (Fig. 6), it did not exceed 22% at the end of the experiment (ballooners:  $21.7 \pm 2.89\%$ ,  $n = 13$ , non-ballooners:  $20.0 \pm 8.66\%$ ,  $n = 12$ , difference not significant, t-test,  $P = 0.77$ ). The surviving animals caught prey in their orb webs and showed normal development with up to four molts within the experimental time.

Using our protocol, we could initiate the full sequence of ballooning behavior promptly in every experiment. The *A. bruennichi* spiderlings always showed an identical sequence of pre-ballooning and ballooning behavior (Fig. 1–4). When exposed to the heat from the lamp, they displayed the "ballooning drive"



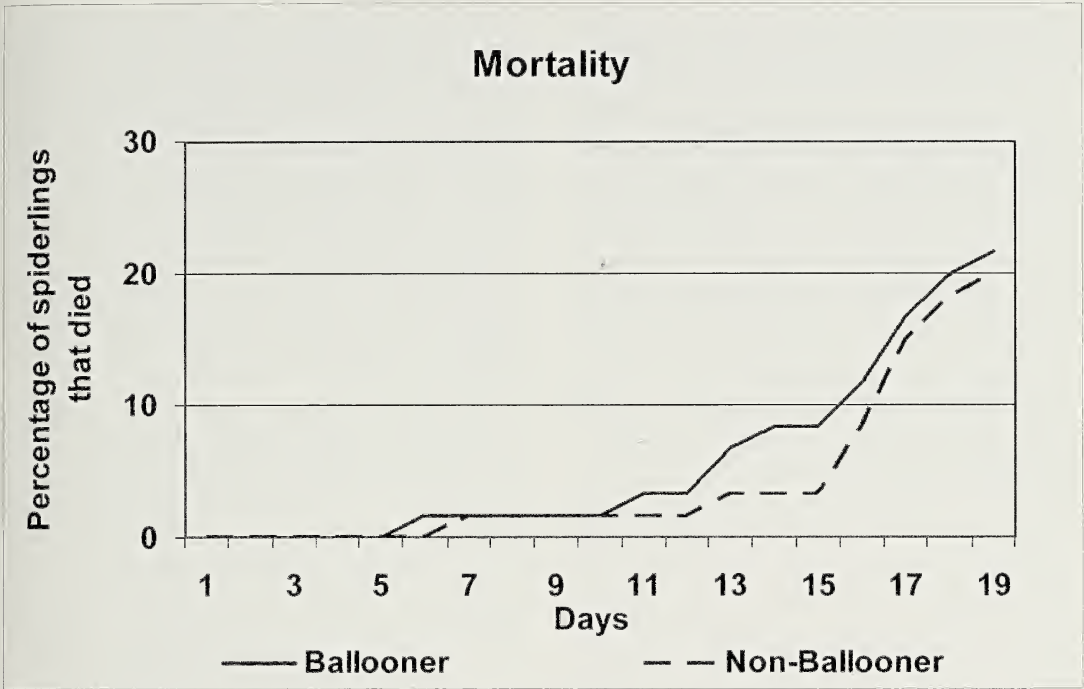


Figure 6.—Mortality of the *A. bruennichi* spiderlings during laboratory rearing.

behavior. Individuals walked to the margin of the spatula, spooled out a dragline and dropped down hanging from the line. While suspended and holding on to the drag line, they let out an additional line of 50–100 cm ballooning silk (Fig. 1). When this was lifted by the breeze generated by the fan and the heat source, the spiderlings cut the dragline and became airborne (Figs. 2, 3). After landing (Fig. 4) they hauled in the ballooning line, formed it with the legs into a silk blob and finally ate the silk, bringing the ballooning behavioral sequence to completion.

Tolbert (1977) observed two modes of preparation for ballooning in sympatric field populations of *A. trifasciata* and *A. aurantia*. A spiderling attempting to become airborne climbed to the top of some blade of grass or other structures and adopted the typical “tip-toe” posture by depressing the cephalothorax and elevating the opisthosoma. Multiple silk lines were then exuded from the spinnerets. When moving air generated sufficient silk, the spiderling became a “ballooner” (Nielsen 1932; Richter 1970; Eberhard 1987). Alternatively, the spiderling could become airborne by dropping and hanging from a dragline, spinning a ballooning thread, which then grad-

ually lifted and lengthened in the breeze. The ballooner then cut the dragline and floated off into the air (Nielsen 1932; Bristowe 1939).

*Argiope bruennichi* can display both pre-ballooning modes. However, the drop and dragline mediated ballooning seems to be more frequent (Follner & Klarenberg 1995). In the field, second-instar spiderlings usually attach the draglines to tips of grass blades or they use silk threads which connect the tips of grass haulms as attaching points (Follner & Klarenberg 1995). In our experiments, we offered individual spiderlings optimal starting conditions, and we never observed the tip-toe ballooning mode. Follner (1994) suggested that “tip-toe” might be a tactical alternative for individuals in unfavorable starting points (e.g., overcrowded tips of grass blades).

Our results show that it is not necessary for spiderlings of *A. bruennichi* to engage in aerial dispersal before building a prey-capture web. While ballooning is frequent in the field (Follner & Klarenberg 1995), it is clearly not an obligate part in the development of this species. In spite of the rapid expansion of the species over the past decades and the potential importance of aerial dispersal for colonizing new habitats, the role of ballooning in *A.*

*bruennichi* does not differ from *A. trifasciata* and *A. aurantia* where this phase in life history is also not obligate (Tolbert 1977).

The mortality of about 20% after 19 days in both experimental groups (difference statistically not significant) suggests that rearing of *A. bruennichi* spiderlings to adulthood may be challenging. Our rearing method based on a diet with *Drosophila melanogaster*, similar to Müller & Westheide (1993), worked well for our purpose, where we only tested the effects of ballooning in second-instar spiderlings on their ability to make their first web.

On average, more than eight days elapsed before *A. bruennichi* spiderlings began to build their first prey-capture web. This appears to be a surprisingly long period, because the animals can only feed once the first web is built. We cannot exclude that this is a laboratory artifact, for example due to unattractive sites for web construction. However, the long latency did not interfere with the rearing regime. The animals appeared to be well adapted to temporary starvation because the mortality was low in this phase (Fig. 6). Also in the field, the spiderlings do not immediately start with prey-capture web construction (Follner & Klarenberg 1995) and endure extended periods of starvation. *Argiope* spiderlings easily survive several days nearby their cocoons, sometimes with communal meshworks of interlocking dragline threads ("communal tangles") (Tolbert 1976, 1977; Follner & Klarenberg 1995) where they find shelter until favorable weather or microclimate conditions allow for ballooning (Tolbert 1977; Follner & Klarenberg 1995; see also Suter 1999 for physics of ballooning).

*Argiope* spiderlings actively select suitable web sites by ballooning, re-ballooning or walking (Enders 1973; Tolbert 1977; Follner & Klarenberg 1995). Also in this nonpredatory phase the spiderlings must avoid starvation. Tolbert (1976) kept *A. aurantia* spiderlings in the laboratory without food and water. Mortality remained moderate in these experiments for several days and only increased distinctly about two weeks after hatching.

The behavioral ballooning sequence could be easily triggered under artificial conditions in our study, suggesting that it will also occur in the field whenever environmental conditions allow. Therefore dispersal and population structure will be primarily driven by mi-

croclimatic conditions in the local habitats. The local persistence of non-emigrants (non-ballooners and short-distance ballooners) in *A. bruennichi* populations might facilitate aggregated dispersion patterns, just as in weather phases which are unfavorable for aerial dispersal. Given ballooning is a less effective means of long distance dispersal than previously thought (Roff 1981; Decae 1987; Wise 1993; Bonte et al. 2003), this could also explain the genetic differentiation among habitat patches in other *Argiope* species (Ramirez & Haakonsen 1999).

The role of natural selection in range expansion has recently been discussed for insects in the context of global warming (e.g., Pimm 2001; Thomas et al. 2001). However, improving environmental conditions at range margins can initiate range extensions purely on the basis of ecological, physiological and population-dynamic processes not requiring any evolutionary change (Thomas et al. 2001; see also Coope 1995; Williamson 1996). Our results are in line with these views and reject the hypothesis of Follner & Klarenberg (1995) that evolutionary processes have changed ballooning behavior in newly founded populations.

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## CAN SIMPLE EXPERIMENTAL ELECTRONICS SIMULATE THE DISPERSAL PHASE OF SPIDER BALLOONERS?

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**ABSTRACT.** Here we describe the structure of a fall speed chamber designed to measure, with low experimental error, the terminal velocities (fall speeds) of spiders of known weight and a given length of silk. We also describe the construction of a simulated individual (SI) which could later be used to estimate the distance travelled by ballooning spiders in the field. Our data and analysis suggest that *Oedothorax* spp. (Linyphiidae) and *Pachygnatha degeeri* (Tetragnathidae) individuals have fall speeds that can be described by their silk length and mass. Of the observed deviance in the fall speeds, 73.7% could be explained by a GLM model common to both species groups. Overlaying the SI fall speed data on this GLM surface suggests that the SIs have similar fall speed behaviors to spiders. However, further estimation is necessary before SIs could be considered valid models for evaluating spider ballooning distances.

**Keywords:** Dispersal, ballooning, schottky diodes, silk, fall speed chamber

Ballooning research has faced a seemingly intractable question for over 300 years: how far do ballooning spiders disperse once airborne? While there have been attempts to observe ballooning distances visually, which suggest that spiders move no more than a few hundred metres in any one attempt (e.g. MacCook, 1877; Follner & Klarenberg 1995; Schneider et al. 2001), it also may be inferred from anecdotal evidence that spiders also make journeys of several hundred kilometres (Yoshimoto & Gressitt 1960; Okuma & Kishimoto 1981). However, such visual and anecdotal data are rare and have yet to yield any significant data for the great majority of ballooning spiders, including the linyphiids (Bell et al. 2005). Although models of ballooning distance have been constructed (e.g. Thomas et al. 2003), the predicted distances have yet to be verified.

The lack of progress is perhaps surprising given recent advances in radar technology (Chapman et al. 2003). Although Rothamsted Research's vertical looking radar (VLR) can measure the horizontal speed, displacement direction, body alignment, mass and shape of

flying insects up to 1 km above ground level (Chapman et al. 2003), as yet ballooning spiders cannot be uniquely identified. The VLR fails to resolve ballooners because spiders lack distinctive allometric ratios and tend to have masses near or below the critical threshold for the radar (Chapman et al. 2003; Jason Chapman pers. comm.).

Recently, indirect molecular genetic techniques have been employed as an alternative to measuring airborne spiders directly (Goodacre 2004). This approach was designed to detect the effect of dispersal rates on the genetic diversity of a number of key linyphiid populations across the British mainland and its islands. The research has shown that populations on islands have lower genetic diversity than those found on the mainland, implying changes in gene flow with isolation distance and island size. It should be noted however, that these findings were not independent of *Wolbachia* infections which confounded observed gene flow measurements. Other molecular studies, which indirectly estimate ballooning distance using gene flow, have been conducted (as reviewed by Bell et al. 2005)

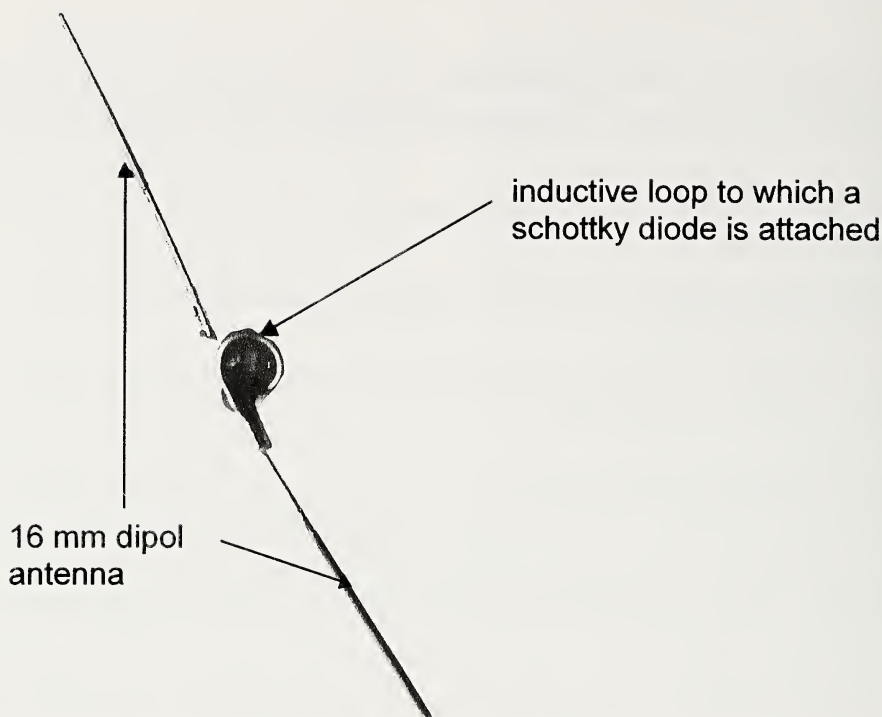


Figure 1.—A simulated individual, which shows a 16mm dipole antenna attached to an inductive loop. The 0.3mm schottky diode (not visible) is fixed to the inductive loop using gold spatter technology. The complete unit weighs 8mg.

but have not yielded estimates for the distances travelled by individual spiders.

We present an alternative approach, based upon synthetic models for spiders that we term simulated individuals (SI). SIs show great promise because they are traceable and biologically inert, thus resolving problems of airborne detection and *Wolbachia* infection. However, while we have begun to understand the physical properties of spiders and their implications for ballooning (Suter 1991, 1992, 1999), the properties of SIs are unknown and their comparative behavior remains untested. In this paper, a description of the technology and data used to compare SI properties against spiders is presented, concluding with a discussion of future research prospects for ballooning.

## METHODS

### Simulated individuals and spiders.—

Males and females of *Oedothorax* spp. (mixed *apicatus*, *fuscus* and *retusus* species: Linyphiidae) and *Pachygnatha degeeri* (Tetragnathidae) have been recorded ballooning many

times (see world catalog in Bell et al. 2005). These species were used as model ballooners for comparison with a simulated individual (SI). While the properties of an SI are yet to be established, the desirable traits should be that it: i) is structurally similar to a spider, consisting of a body and an associated silk component; ii) is able to generate its own drag to enable it to become airborne; iii) is traceable, producing an automated signal of its location; iv) allows manipulation of the silk component to known levels of drag; and, lastly v) is a 'null' spider with no behavior which minimizes drag variability (i.e. absence of biting and reeling of the silk line and reduced body posture modification). Schottky diodes, mounted onto an inductive loop with a dipole antenna (referred to as 'diodes' hereafter) have the potential to offer these properties, despite having none of the physical attributes of spiders (Fig. 1). We used 8 mg diodes in the following experiments.

Spiders create drag with single or multiple silk lines that may account for 75% of the total drag of the spider (Humphrey 1987). For



the diodes, simulated silk was adopted initially as a replacement for natural silk. Titanium-coated fibre glass was identified as a possible solution and responded positively to very light convection currents (i.e.  $< 1$  m/s). However, it proved to be fragile despite being four times the diameter (400 nm) of natural linyphiid silk (e.g. *Tenuiphantes tenuis* 100 nm). In light of these flaws, we used natural silk. Although linyphiid silk is too fine to manipulate easily, it was possible to attach the drag line silk of immature *Araneus diadematus* (Araneidae) to the diodes. For both spiders and diodes, all individuals were weighed before being introduced to the Rothamsted fall speed chamber described below. In total, 38 spiders (*Oedothorax* spp.  $n = 13$ ; *P. degeeri*  $n = 25$ ) and 4 diodes were dropped attached to silk lengths within the range of 0–2.3 m.

**Rothamsted fall speed chamber.**—The physical structure of the 9 m vertical chamber was relatively simple and included three detector stages and a hotwire (Fig. 2). The hotwire was used as a silk-shearing mechanism to allow suspended spiders to be dropped without human intervention. The first detector stage was used to manipulate the silk length, between 0.11 m and 2.3 m, at which a suspended spider or diode entered free fall and the two remaining stages measured the fall speed of each individual having reached terminal velocity. As a precursor to entering the chamber, spiders were first prompted to drop down on a drag line from an oscillating probe. Having produced a dragline of  $>10$  cm, spiders were then fixed to the hotwire and allowed to pay out more silk until triggering the first detector stage (Fig. 3). In separate experiments, the diodes were suspended on fixed lengths of silk placed on the hotwire. The silk was sheared by one of two methods: either a) the spider broke the first detector stage light beam which automatically triggered the hotwire (Figs. 2 & 3); or, b) if shorter lengths of silk (i.e.  $< 0.11$  m), silkless drops or fixed drops with diodes were required, a PC-operated drop mechanism which manually triggered both the three detector stage light beams and the hotwire to an 'on' position was used. After either the hotwire or manual drop had been triggered, the spider or diode entered free fall for at least 5.4 m (i.e. depending on the first detector stage height) until it was measured passing through the second detector

stage at terminal velocity when timing started (Fig. 2). Timing was stopped, and the fall speed computed, when the individual passed through the third detector stage.

The hardware environment behind the fall speed chamber measurements is based on the simple principle that when an object breaks a light beam, a passive record can be logged at a given point in time. Technically, the chamber included its own microprocessor controller based on a PIC16F876 running at 20 MHz and programmed using CCS PICC compiler (Fig. 4). This controller was connected to a PC running dedicated software through a RS232 port, which allowed the user to control the light source and silk release mechanism (i.e. automatic/manual release) remotely. All control outputs were by opto-isolated open drain mosfet drivers. The hardware detected falling objects through the use of a medium area photo diode (41.3 mm<sup>2</sup>) connected to a two stage high gain amplifier. A first order bandpass filter was used to remove unwanted signals below 300 Hz and above 5 KHz. The photo diode was mounted in a black box, with one end cut off, to help prevent ambient light interfering with the source light. The initial design for the detection system was to incorporate a laser diode with line generator lens as the light source. However, the tested lasers were found to have a small but significant fluctuation in their output which made it impossible to distinguish the object signal from noise when used in conjunction with the detection circuit. The circuit will need to be redesigned before lasers can be used in this application.

As an alternative, high power quartz halogen bulbs (60 W) were used in conjunction with two 0.8 mm slits spaced at about 160 mm apart so that a reasonably fine line beam could be produced (Fig. 5). To focus the light onto the photo diode, Fresnel lenses ( $\sim 300$  mm wide, cut from a 280 mm square lens along the diagonal, 50 grooves per inch and a focal length of 234 mm) were employed. The signal from the photo diode was then amplified and filtered before being applied to the single input channel of the analogue switch driven by a free running 3 KHz quartz clock (Fig. 4). The two output channels of this switch were then applied to the inputs of the voltage comparator. Any low frequency variation of the input signal due to amplifier drift or ambient light falling on the photo diode was ignored

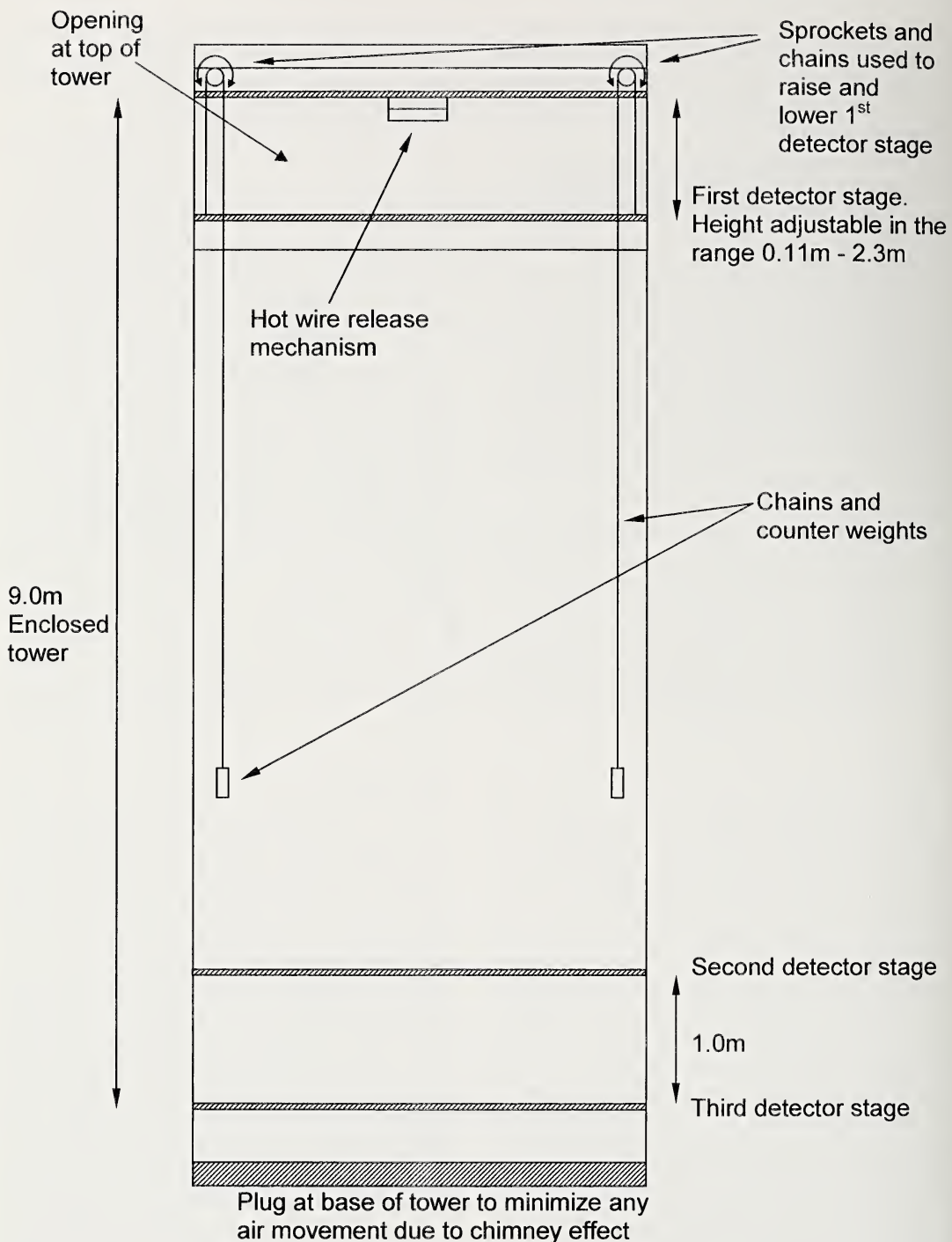


Figure 2.—Side view of the Rothamsted fall speed chamber.

by the comparator. However, any object passing through the light beam produced a much faster change in signal level which triggered the comparator. The comparator output was used

as the trigger input to the microprocessor controller. The inherent precision of the microprocessor quartz clock ensured that the accuracy of the system fell within at least  $\pm 1$  ms



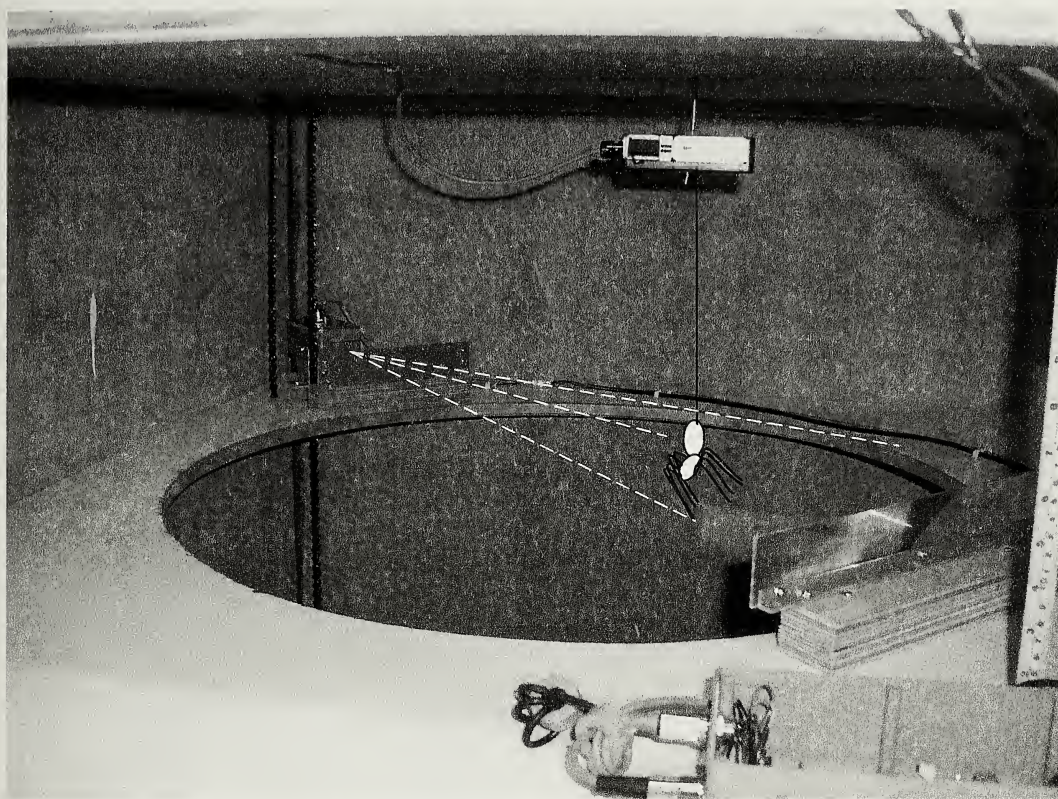


Figure 3.—Top of Rothamsted fall speed chamber showing the hotwire release mechanism to which a spider is suspended on a silken line.

(accuracy checked against a calibrated Systron Donner counter timer type 6250A) and represented a fall time recorder error of the spiders sampled between 0.0046–0.055%.

**Statistical analysis.**—Fall speeds were analyzed using a Generalized Linear Model (GLM), the Normal distribution and the log-link function in Genstat (version 6, VSN international, Oxford, UK; McCullagh & Nelder 1989).  $\log_{10}(\text{Silk Length} + 1)$  was fitted in the model as the explanatory variable, with spider species and  $\log_{10}(\text{Spider Mass})$  as covariates. The model fit was checked for overdispersion in the data (McCullagh & Nelder 1989). The model's standardized residuals were checked for linearity, leverage and homogeneity (McCullagh & Nelder 1989). No attempt was made to fit a GLM to the provisional data for the diodes.

## RESULTS

The GLM was found to fit the spider fall speed data extremely well, explaining some

73.7% of the GLM deviance observed (Fig. 6). The data were found to be underdispersed, suggesting that the data were more regularly distributed than expected for data conforming to the Normal distribution. An empirical scale parameter was used to adjust the model fitted estimates of error to account for this underdispersion (see McCullagh & Nelder 1989).

Spider fall speeds were found to decrease with increasing silk length ( $t_{1,36} = 2.87$ ,  $P = 0.004$ ) and increase with an increase in spider body mass ( $t_{1,36} = 3.25$ ,  $P < 0.001$ ). There was no interaction between silk length and spider body mass ( $t_{1,36} = 0.28$ ,  $P = 0.78$ ). No difference in the GLM was found with spider species ( $t_{1,36} = 0.70$ ,  $P = 0.49$ ), and no interaction was found between spider species and silk length ( $t_{1,36} = 0.62$ ,  $P = 0.53$ ) nor spider weight ( $t_{1,36} = 1.31$ ,  $P = 0.19$ ). Thus, a common GLM was applicable to both *Oedothorax* spp. and *P. degeeri*:

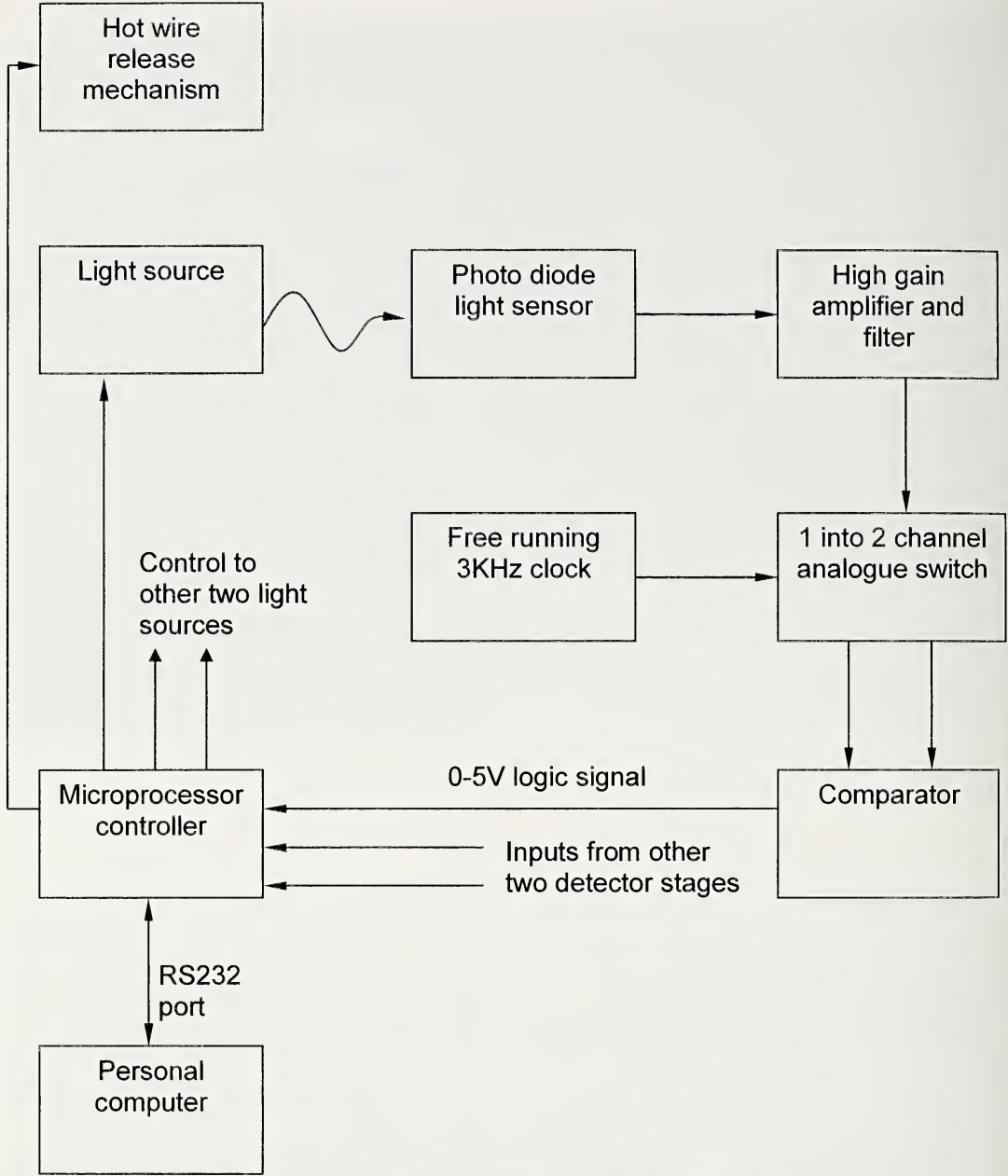


Figure 4.—Block diagram detailing system electronics.

$$\log_{10}(\text{Fall Speed}) = 3.83$$
$$- 0.95\log_{10}(\text{Silk Length} + 1)$$
$$+ 1.11\log_{10}(\text{Spider Mass})$$

Spider sex was a non-significant model covariate ( $t_{1,36} = 0.06$ ,  $P = 0.95$ ). However, the *Oedothorax* spp. are sexually dimorphic

with respect to weight (females =  $2.4 \pm 0.3$  mg; males =  $0.8 \pm 0.004$ ;  $F_{1,11} = 50.14$ ,  $P < 0.001$ ), yielding sex specific fall speeds for a given silk length in this species group. We plotted the fall speeds for diodes over the GLM in Fig. 6. The overlaid data suggests that diodes behave in a manner that is analogous to the spiders.



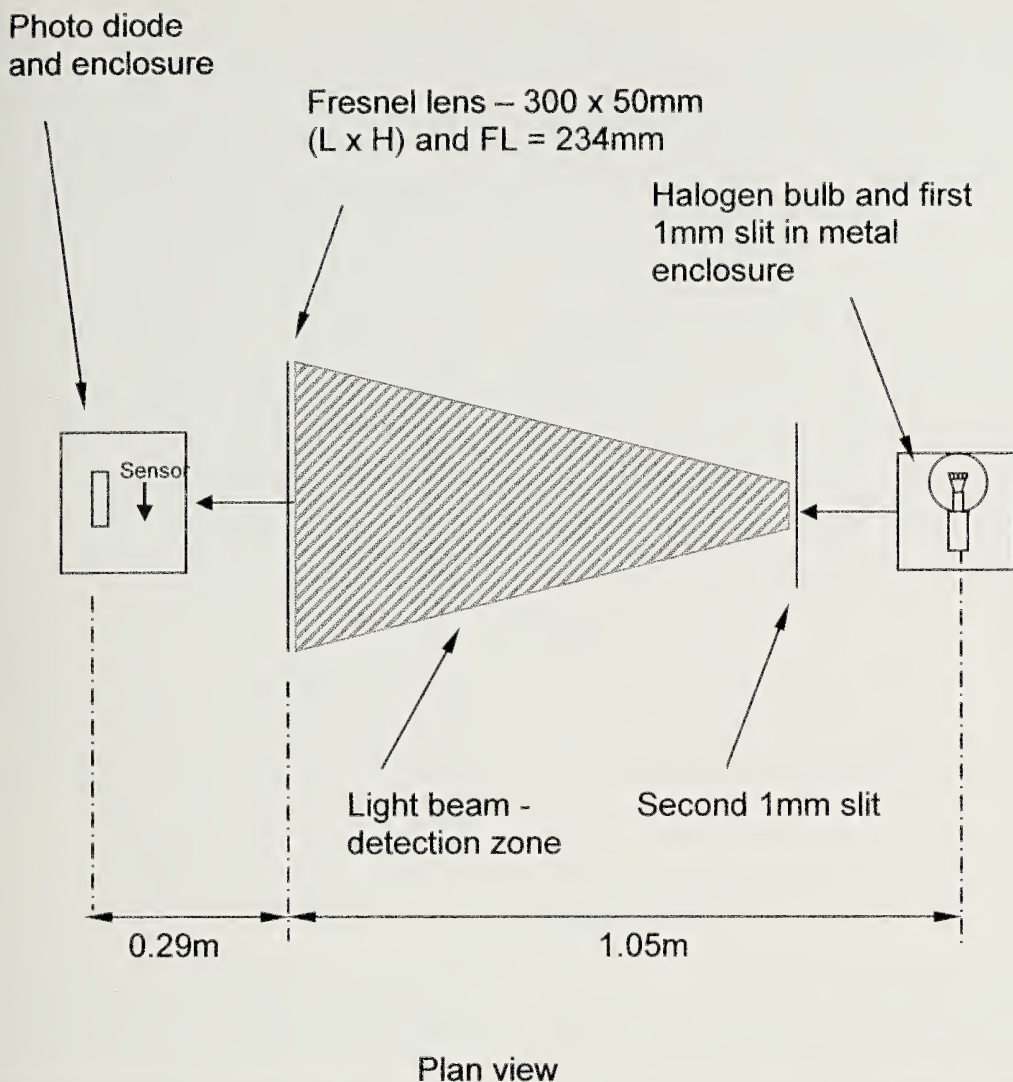


Figure 5.—Diagrammatic view of the filtered light source (←) producing a large detection zone which is constantly monitored by the photo diode.

## DISCUSSION

### Rothamsted fall speed measurements.—

This experiment unequivocally demonstrates that natural spider silk can be attached to diodes and that drag, and consequently fall speeds, can be systematically manipulated through the length of the silk line. The observed positive relationship between drag and silk length for SIs was analogous, but not identical, to spiders in free fall. Despite the limits of the provisional data presented, our results are supportive and imply that these diodes represent a simple, yet viable paradigm of real spiders. Encouragingly, these diodes

have the potential to develop our understanding of spider ballooning far beyond our present knowledge.

Spider ballooning research is limited, although scientists are aware of the importance of silk in ballooning (Bell et al. 2005). For example, the effect of silk length on the fall speeds of spiders (Suter 1991), moth larvae (Lepidoptera) (Batzner 1968; Barel 1973; Mitchell 1979; McManus & Mason 1983; Ramachandran 1987) and spider mites (Tetranychidae) (Jung & Croft 2001) has already been demonstrated. Of these, Suter's (1991) seminal research attempted to evaluate fall

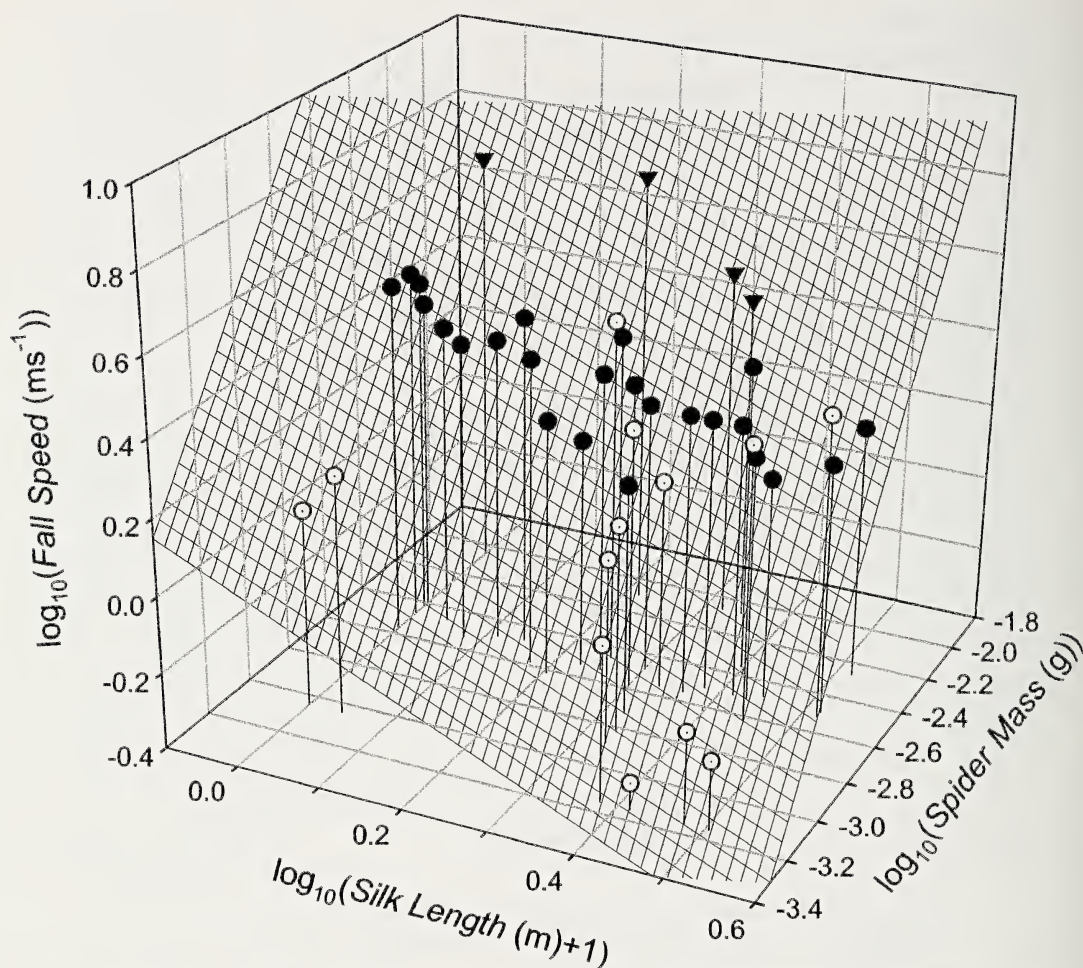


Figure 6.—Observed fall speed data for individuals of *Pachygnatha degeeri* (●), *Oedothorax* spp. (○) and diode (▼) against silk length and spider mass. The hatched surface represents the GLM fitted model for fall speeds with silk length and spider mass.

times independently of human error. Even so, fall speeds still had to be estimated by extrapolation because of the short fall distances in Suter's experimental chamber. The advantages of the Rothamsted fall speed chamber are that measurements may be taken in near-still air conditions and when they have reached their terminal velocity, after individuals have fallen at least 5.4 m. Despite this, the results are subject to error due to spider behaviors when falling. Here no attempt was made to control for postural variation, such as spreading or withdrawing legs, which has been estimated to have up to a 10 fold effect on body drag (Suter 1992). Postural control may also be important in mites which manipulate drag in a similar fashion to spiders and may be able to

influence where they land (Jung & Croft 2001). Such postural control could account for some of the unexplained variation in our GLM and may be estimated by placing digital cameras inside the Rothamsted fall speed chamber. The posture of the photographed spiders, once categorized by shape, might then be included as a third covariate within the GLM. However, this behavior might only be expected to account for a maximum of 25% of the observed variation (deviance) in the fall speed data (Suter 1991; see also Humphrey 1987).

Allowing spiders to reach their terminal velocities over a comparatively large distance simplifies the mathematics of calculating terminal fall speeds, but also has the potential to be biologically erroneous. Purely from obser-



vation during handling, both species tested were able to pay-out silk at a rate of  $>1$  m/s, particularly when individuals adopted 'escape' behaviors. If this paying-out of silk occurred during freefall, then the lightest individuals could produce several meters of 'undetected' silk length during their fall. In practice this is unlikely, given that the residual variation was relatively small. While it is important to highlight posture and silk reeling as sources of error, they are inescapable covariates of spider ballooning. Posture variation might be standardized, though not removed, by anaesthetising individuals with carbon dioxide before entering the chamber (Jung & Croft 2001). However, this would have an impact on an individual's ability to produce silk. The solution to evaluating the effects of posture and variation in silk length during freefall can only be to increase the number of observations (replicates).

Suter (1991, 1992) recognized the importance of spider mass, which served to increase the fall speeds at a given length of silk. Mathematical models which seek to determine the probability of dispersal based on a species by species account, also need to parameterize mass and consider sex as a covariate where obvious differences in males and females occur. As far as we are aware, this has been ignored to date.

**The future of schottky diodes to simulate the dispersal phase of spider ballooners.**—This research has shown that simulating ballooners has potential. Natural silk attached to diode bodies produces drag in a manner directly analogous to a spider. Scanning harmonic radar has been shown to be effective in tracking diode-tagged bees for up to 900 m from the radar station (Osborne et al. 1999). To follow SIs, the use of a similar scanning radar set-up is planned. Using this technology we can explore unanswered questions including; how far do ballooners travel; and, what is the pattern of dispersal of ballooners within a 1–2 km range? However, our research is at an early stage. While releasing diodes in the field is the ultimate objective, several aspects of SI behavior need further estimation before SI ballooning data can be captured. Notably, the dependence of fall speeds on diode mass requires evaluation because the 8 mg diodes used do not represent the majority of ballooners, which are under 2 mg (Greenstone et al.

1987); although much heavier spiders can be found ballooning. Reducing schottky diode mass by at least 75% would affect the drag dramatically and could require models for SIs that differ significantly from that estimated here for spiders. Only after completion of this diode model estimation phase of the project could radar-based fieldwork follow.

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## NOCTURNAL NAVIGATION IN *LEUCORCHESTRIS ARENICOLA* (ARANEAE, SPARASSIDAE)

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**ABSTRACT.** When the males of the Namib Desert spider *Leucorchestris arenicola* (Araneae, Sparassidae) reach the adult stage they undertake long nocturnal searches for females. From these searches they return to their home burrow often in a straight line only retracing a fraction of their outward path if at all. Distances of 40 m and 13 m are conservative estimates of the mean round trip length and maximum distance from the burrow. Returning to the starting point of a round trip of such length is theoretically only possible if the navigator uses external cues for positional reference. The possible involvement of a range of external cues in the male *L. arenicola* was investigated. The direction of gravity, the sun, polarized sunlight, olfaction, constant wind direction and vibrational beacons are ruled out or deemed unlikely to be involved in the spiders' homing.

**Keywords:** Homing, egocentric, geocentric navigation, path integration, dead reckoning

Complex long distance navigation by arthropods is usually associated with the formidable navigational capabilities of the eusocial hymenopterans such as bees and ants (e.g., von Frisch 1967; Wehner 1992). In spiders long distance traveling is most often done by ballooning involving extrusion of silk threads into the air (Suter 1991). This form of transportation is, however, only used by relatively small spiders. In large spiders such as the mygalomorph spider *Aphonopelma hentzi* Girard 1854 (Araneae, Theraphosidae) travels over long distances are by walking rather than ballooning. However, these spiders only do one-way excursions without returning to the starting point (Janowski-Bell & Horner 1999). Keeping a straight line so as not to end up at the starting point, which may represent an area where resources are overexploited or an area not well suited for a given life stage, might require actual navigation (Dacke et al. 2003). However, returning to the starting point of an excursion, i.e. showing homing behavior, is a far more demanding navigational task for an animal than a long walk in a chosen direction.

In spiders, studies of homing have so far been reported to occur over distances of less than a meter (Seyfarth & Barth 1972; Seyfarth

et al. 1982; Görner & Class 1985; Dacke et al. 2001). However, in the central Namib Desert a spider shows impressive skills of navigation. Henschel (1990, 2002) was the first to notice that the adult males of *Leucorchestris arenicola* Lawrence 1962 (Araneae, Sparassidae), like foraging bees or ants, also return to the starting point after excursions over distances of tens of meters on the desert floor.

The purpose of the present account is to outline the current state of knowledge about the mechanisms used or not used in the long distance homing navigation of *L. arenicola*, show new results concerning the role of vibrational beacons, and finally point out the most promising leads that will be followed in future experiments.

### *LEUCORCHESTRIS ARENICOLA* AND ITS MOVEMENT PATTERNS

*Leucorchestris arenicola* is an endemic sparassid (Jäger 1999) of the Namib Desert. It is a large spider weighing up to 5 g (Henschel 1990), heavy enough to leave footprints in the sand (per. obs.). Adult males have standing leg spans often exceeding 10 cm (Fig. 1). Adult females have shorter legs but are usually slightly heavier than the males. Adult males comprise up to 12% of the population and occur only in the summer period (September–April) (Henschel 1990). The spiders dig 30–

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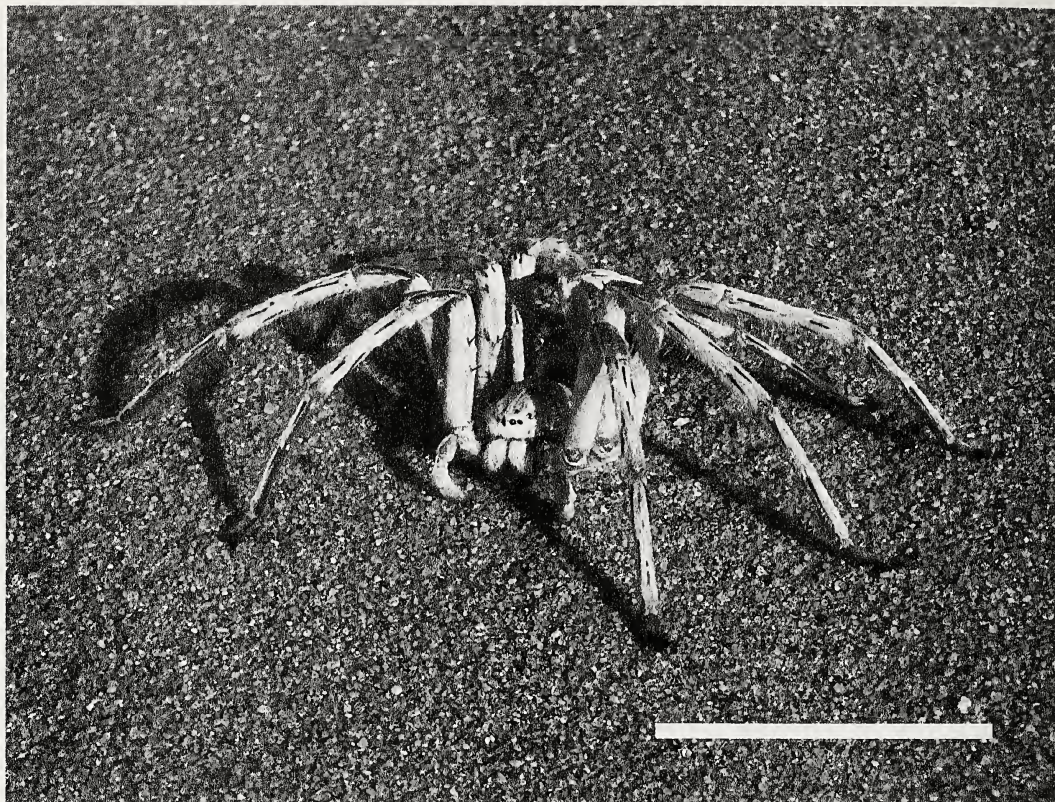


Figure 1.—Adult male *L. arenicola* showing protective coloration against the dune sand. Scale bar: 5 cm.

40 cm long burrows in the sand at an angle of ca. 30 degrees (Henschel 1990). This gets the spider to a depth of approximately 25 cm where climatic conditions are far more tolerable than on the desert surface (Henschel 1990). They are strictly nocturnal spiders, most frequently first becoming active an hour after sunset (Fig. 2). This was established using infrared beam sensors and time-event data loggers (TinyTag). The beams were placed so they crossed the entrance of the burrows. Thereby the time a spider left the burrow was recorded. This activity pattern is probably an adaptation to the high temperatures in the desert during the day and the relative absence of predators at night (Cloudsley-Thompson 1983; Henschel 1990). Like many nocturnal desert spiders they have a light color rendering them inconspicuous against the desert sand (Cloudsley-Thompson 1983; Dippenaar-Schoeman & Joqué 1997). In the desert, the spider is found at the dune base where the sand is more stable and less stony compared

to the slip face of the dunes and the gravel plains found between the dunes (for definitions of dune habitats see Robinson & Seely 1980). The spiders are highly territorial and defend an area with a radius of 3–4 m from their burrow (Henschel 1990; Birkhofer 2002). Especially burrow construction by another spider triggers strong aggressive behavior from a territory owner (Birkhofer 2002). Females and immature spiders mainly restrict their surface activity, e.g., prey capture, to within their territories. The main prey is tenebrionid beetles. The prey are killed on the desert surface and then dragged into the burrow (Henschel 1994). At the time the immature spiders disperse from their maternal burrow or when an adult female leaves her offspring, they may walk beyond their 3–4 m territory boundaries. However, these are one-way trips over distances far shorter than the roundtrip of the adult males. Observing the tracks of the spiders, it quickly becomes clear that adult males truly are the ones that regu-



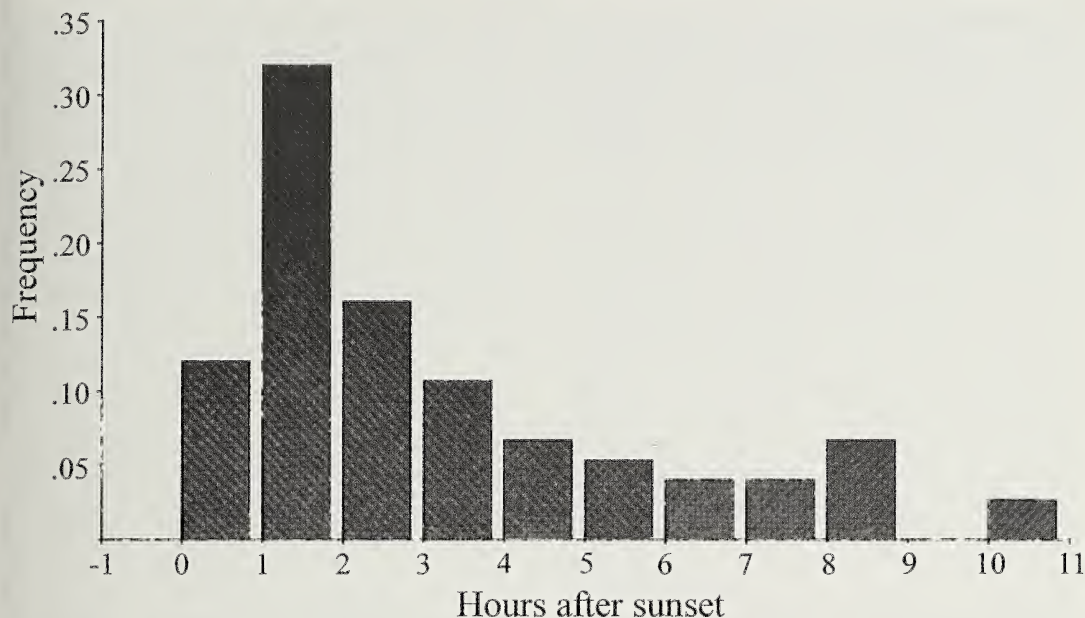


Figure 2.—Frequency of appearances from the burrows on the desert surface by male *L. arenicola* ( $n = 75$ ) in relation to sunset (0 = sunset). Activity recordings were made with infrared beam sensors and time-event data-loggers.

larly wander far. The adult male spiders' tracks can easily be identified by the size of the leg span and the conspicuous drum and scrape marks often seen on the paths (pers. obs.).

When reaching the adult stage the male *L. arenicola* begins making long excursions searching for mating opportunities. These searches for the burrows of adult females are trips several orders of magnitude larger than the spiders' body size and over far longer distances than their average territory size and were, therefore, described as long-distance excursions (Henschel 2002). The general layout of the male spiders' excursions can be divided into two sections: an outward path and a return or homing path. The outward path is characterized by a meandering and occasionally very tortuous searching walk, while the return often is a straight line walk heading towards the burrow across ground not covered on the way out (Fig. 3).

By examining the general movement pattern of the male *L. arenicola* and drawing upon information from other navigating arthropods, especially spiders, we can list the probable methods male *L. arenicola* uses for homing.

#### HOMING NAVIGATION

Theoretically, a male *L. arenicola* could navigate to and from his burrow using two principally different methods. The spider could use either a geocentric or an egocentric system of references for determining his position. If navigating by geocentric cues, the male spider must determine his position relative to his burrow using landmarks in the surroundings. This requires memorization of a topographic map of the surroundings, also known as a cognitive map (Tolman 1948). The use of such a map has been suggested for honey bees (Gould 1986). So far however, the evidence for this has not been conclusive and the behavior of navigating arthropods studied has been explained by simpler mechanisms than a memorized topographic map (Wehner & Menzel 1990). In such a non-map fashion, landmarks in the surroundings and the contour they present against the horizon are used in homing by wood ants (*Formica japonica*) (Fukushi 2001; Fukushi & Wehner 2004).

If doing egocentric navigation the spider should assess his position in relation to his burrow by using information collected while he is walking. Therefore, instead of having a

map, the navigator continuously keeps track of all distances and directions traveled using this information to "calculate" the direction towards the burrow. This form of navigation is called dead reckoning or path integration (Mittelstaedt 1985).

The necessary information about distances and directions steered can be obtained either ideothetically or allothetically (Mittelstaedt 1985). These two methods may be employed simultaneously. Ideothetic path integration implies that the spider navigates based entirely on internally gained information (Mittelstaedt 1985). This has been shown to be the case in the homing of the ctenid spider *Cupiennius salei* Keyserling 1877 which can return to its refuge using only information gathered from the lyriform organs (Seyfarth & Barth 1972). Pure ideothetic navigation is, however, susceptible to accumulation of errors ultimately leading to severe loss of precision. It is, therefore, only usable when navigating over shorter distances (Benhamou et al. 1990). When traveling the distances navigated by the male *L. arenicola*, external cues are, therefore, supposedly necessary. Doing path integration and using external cues is called allothetic navigation (Mittelstaedt 1985). A number of external cues are known to be used by several arthropods when they are navigating by use of path integration. The sun and the moon are well-known sources of directional information, used directly or indirectly via the polarized light patterns and spectral gradients they produce in the sky (Tongiorgi 1969; Rossel & Wehner 1986; Wehner 1994, 1997; Wehner et al. 1996; Dacke et al. 1999; Gal et al. 2001; Dacke et al. 2003). The direction of gravity (Bartels 1929; Hill 1979), constant wind direction (Wehner & Duelli 1971) and perhaps magnetism (Ugolini & Pezzani 1995) are also cues used by arthropod navigators. Often more than one of these external cues are used in order to achieve better precision.

#### THE HOMING OF *L. ARENICOLA*

Based on empirical and theoretical grounds several experiments were designed and carried out in search of the external cues used in the navigation of *L. arenicola*. To begin unraveling the mechanisms of homing navigation for male *L. arenicola* it is important to record and analyze paths in detail. A method to record the paths in all three dimensions was therefore

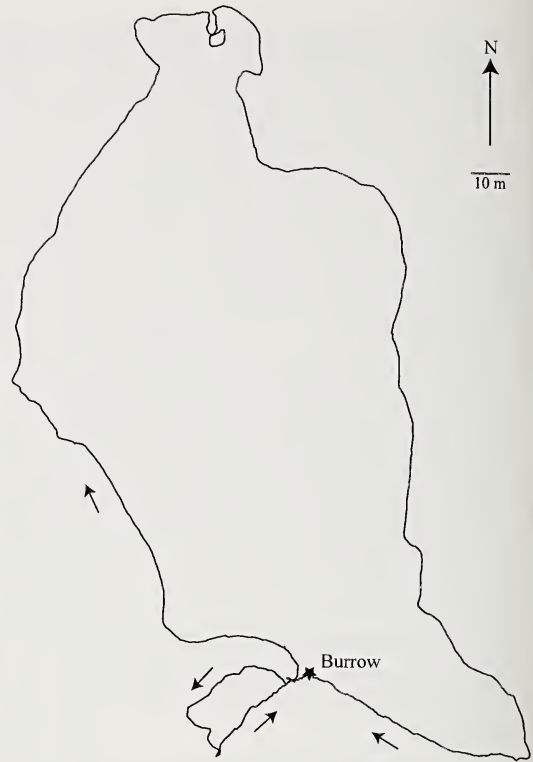


Figure 3.—Trajectory of a single night excursion of a male *L. arenicola* projected onto a 2 dimensional plane viewed from above. Total path length was 810 m.

developed (Nørgaard et al. 2003). A marker was placed along the paths each time the direction of the walk changed by more than the spiders leg span (approx. 5°). This divided the path into segments. The length of each segment was measured using a tape measure, the direction with a compass and the slope with a digital inclinometer (Bosch DNM 60 L). These recordings found a path length (mean  $\pm$  s.e.) of 4092 cm  $\pm$  664 cm and a maximum distance to the burrow of 1313 cm  $\pm$  223 cm (Nørgaard et al. 2003). The longer the path, the more difficult complete tracking becomes. These path measurements were therefore biased towards shorter distances as focus was solely on recording complete round trips. The area in which the recordings took place was densely populated by spiders and naturally bordered by interdune gravel plains and riparian vegetation of the ephemeral Kuiseb river. Recent path recordings in another more open and less densely populated area have found far longer distances traveled by the spiders. An



approximately 810 m long path is the longest detailed round trip excursion recorded to date of any spider (Fig. 3). The ability to record the paths in all three dimensions allowed for an analysis of the slopes encountered by the spiders during their excursions. A constant slope of the substrate, i.e. direction of gravity, could potentially provide the spider with a usable compass during its navigation. However, the sand surface of the desert is corrugated by the wind and no even slope existed, and use of the direction of gravity in the spiders' navigation was therefore ruled out (Nørgaard et al. 2003) (Figs. 4–6).

Long distance homing over ground which was not covered during the outward trip immediately excludes the use of pheromone trails. Direct homing by olfactory means is unlikely to function over the long distances the spiders travel; this is corroborated by observations of spiders having different homing directions on the same night and the occurrence of changing wind directions. Directly using constant wind direction as a compass cue is unlikely for the same reason and because of the turbulence at the surface caused by the sand ripples. Olfactory cues may however still be involved in the final pinpointing of the burrow.

Sand is the major component of the spiders' habitat and one of the physical properties of this substrate is its ability to conduct vibrations as surface waves in the range between 300–500 Hz (Brownell 2001). These frequencies have wavelengths of 9–15 cm (Brownell 2001), and the leg span of *L. arenicola* falls into this range. Some spiders are highly sensitive to vibrations detected by the lyriform organs on their legs (Foelix 1996), raising the possibility that the spiders could derive directional information from a vibration source.

With a geophone one can hear such sand vibrations. If vegetation hummocks have a distinct sound this might create a "sound landscape" with unique "landmarks" or sound beacons usable in the spiders' navigation, in the same way as a visual landmark possibly could. Therefore, an experiment was carried out to investigate whether or not the spiders could be using such sound beacons. Two speakers were buried in the sand as beacons. Beacon A was placed at a distance of 5 m from a male spider's burrow and beacon B was placed 10 m away in the same direction.

An amplifier (Star sound SSA-2040) and a MP3 player (Loomax 300 M), both powered by a 12 V battery, supplied the audio signal for the beacons. A continuous 300 Hz tone audible in the sand from a distance of at least 20 m was emitted from beacon A starting before sunset. At night when the spider had left his burrow beacon A was switched off and beacon B switched on. In this way the position of the beacon was virtually shifted. In nine experiments, each with different males, no effect of switching the position of a sound beacon was found. All spiders behaved as if undisturbed, searching for females, mating, and returning to their burrows as normal. Thus, while these spiders are likely to depend heavily on vibration sensing for prey detection, this sensitivity does not appear to be important for navigation.

Of the celestial cues available to the spiders, only the moon and the polarized light it produces need be considered here as they are strictly nocturnal. Individual bright stars, star constellations or perhaps the band formed by the Milky Way might also be used by the spiders as a compass cue.

#### CONCLUDING REMARKS

Many possible external cues are available to the navigating male *L. arenicola* and, as described above, a number of these have by now been ruled out entirely or must be considered highly unlikely to be involved in the process. Of the possible non-visual external cues, magnetism remains to be tested. Magnetism used for bipolar positional reference may be used by lobsters to return to a specific area (Boles & Lohmann 2003). This is not sufficiently precise to locate a tiny burrow entrance in the desert floor. Moreover, the distances over which *L. arenicola* wanders are probably too short to allow for magnetic navigation. Recent experiment has shown that vision plays a role in the navigation done by *L. arenicola* (unpub. data). Thus, with our current knowledge, a visually based navigation system appears to be the most promising explanation of the remarkable homing behavior of *L. arenicola*. The necessity of visual cues has been shown in the wolf spider *Lycosa tarantula* (Linnaeus 1758) (Ortega-Escobar 2002), even though it is navigating over distances far shorter than what is seen in *L. arenicola*.

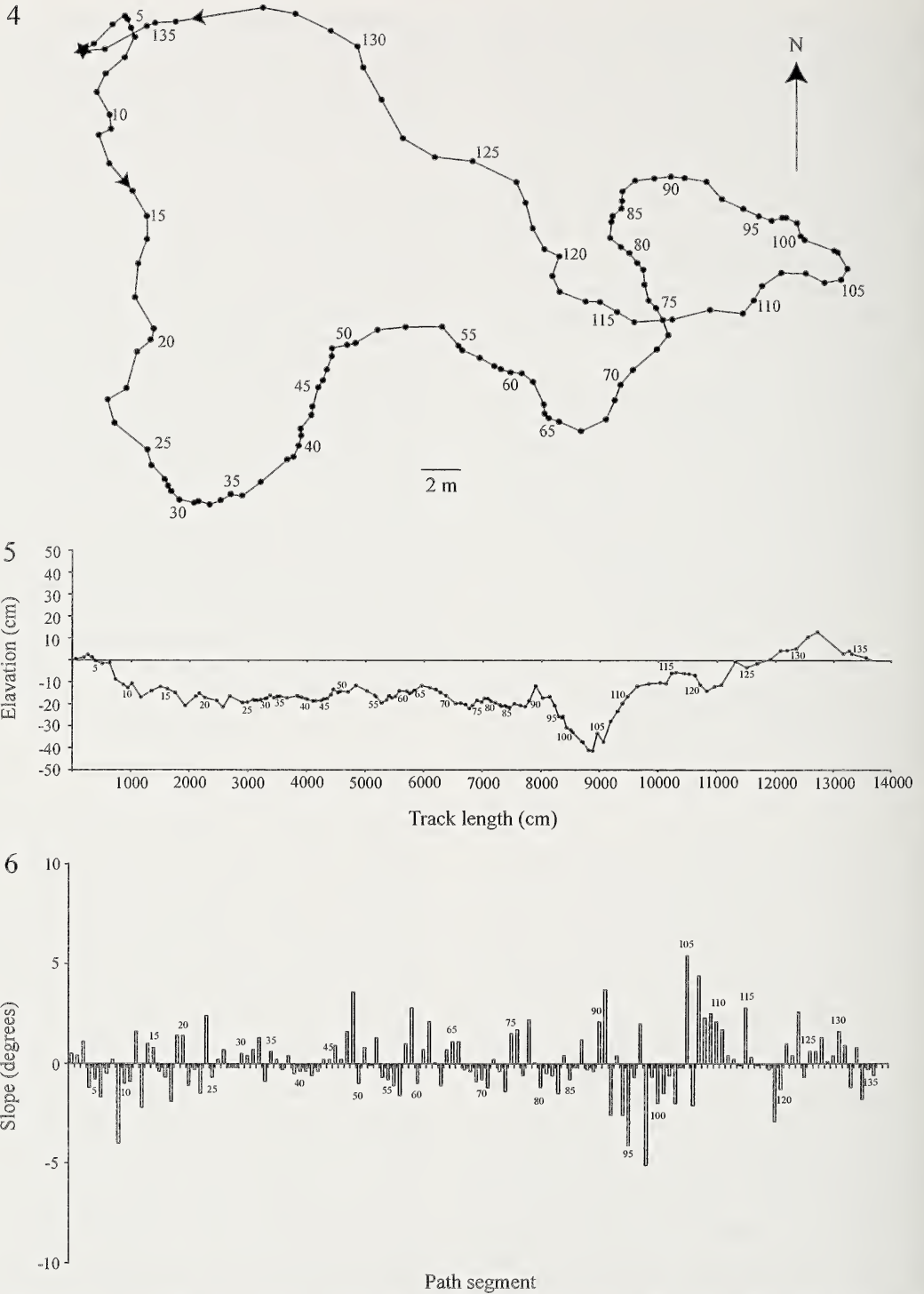


Figure 4-6.—4. Path of a male *L. arenicola* spider projected on to a flat plane. The black star marks the burrow and the arrowheads indicate the direction in which the spider had walked. The small dots along the path each represents a marker put down for the path measurement. The numbers denote every fifth marker and thus path segment. 5. Elevation profile of the spider path illustrated in Fig. 4. The burrow is positioned at the zero elevation line. 6. Histogram showing the slope of each segment of the spider path illustrated in Fig. 4. The 0° line is horizontal. (Adapted from Nørgaard et al. 2003).



The experiments so far have been focused on the compass component of the spiders' navigation mechanism, but path integration also requires an odometer. Many other questions call for investigation. For example, why do the males return to the burrow from which they started out? Is the energy cost of building a new burrow too high because it is necessary to have a deep burrow to survive high daytime temperatures? Or is it simply too risky to build a new burrow because of cannibalism (Henschel 1990; Birkhofer 2002)?

Due to the scale of the excursions, most of the experiments with male *L. arenicola* can only take place in the field. The collection of data is, therefore, subjected to the constraints of the climate of the Namib Desert and the seasonal availability of adult males. These are conditions that may slow down, but not stop, the progress in gaining knowledge about the astounding homing navigation of *L. arenicola* males.

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## USE OF *ANOPHELES*-SPECIFIC PREY-CAPTURE BEHAVIOR BY THE SMALL JUVENILES OF *EVARCHA CULICIVORA*, A MOSQUITO-EATING JUMPING SPIDER

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**ABSTRACT.** The prey-capture behavior of the juveniles of *Evarcha culicivora*, an East African mosquito-eating jumping spider, was investigated in the laboratory using living prey and using dead, motionless lures made from two mosquito species, *Anopheles gambiae sensu stricto* and *Culex quinquefasciatus*. Having tested individuals of *E. culicivora* that had no prior experience with mosquitoes (rearing diet: only chaoborid and chironomid midges), our findings imply that the small, but not the large, individuals of *E. culicivora* have an innate predisposition to adopt *Anopheles*-specific prey-capture behavior. Findings from lure tests implicate posture as a primary cue by which the small juveniles of *E. culicivora* identify *Anopheles*. Each individual of *E. culicivora* was presented with lures, that were either in the posture typical of *Anopheles* or in the posture typical of *Culex*. Small, but not large, juveniles of *E. culicivora* often responded to *Anopheles* mounted in the *Anopheles* posture and *Culex* mounted in the *Anopheles* posture by taking an indirect route or a detour to the prey which enabled the salticid to approach the lure from behind. However, detours were not routine for small or for large individuals of *E. culicivora* when the lure, whether made from *Anopheles* or *Culex*, was in the *Culex* posture. When tested with live mosquitoes, small juveniles of *E. culicivora* were more effective at capturing *Anopheles* than *Culex*. Large juveniles were more effective than small *E. culicivora* juveniles at capturing *Culex*, but large and small juveniles had similar success at capturing *Anopheles*.

**Keywords:** Salticidae, mosquitoes, malaria vectors, predation, detours, predatory versatility

Distinctive prey-specific capture behavior has evolved in at least two groups of jumping spiders (Salticidae), the araneophagic species (i.e. species that prey especially on other spiders) and the myrmecophagic species (i.e. species that prey especially on ants). Sometimes araneophagic and myrmecophagic salticids use specialized tactics to target remarkably specific prey. For example, *Portia fimbriata* (Doleschall 1859) from Queensland (Australia) adopts tactics that are specific to a particular prey species, *Euryattus* sp., a common salticid in the same habitat (Jackson & Wilcox 1990, 1993a). *Euryattus* females are unusual among salticids because they make a nest by suspending a dead rolled-up leaf by silk lines from the vegetation. *Portia fimbriata* captures *Euryattus* females by mimicking the vibratory courtship displays of *Euryattus* males, luring the females out of their leaf nests.

Here we consider another example of remarkable predatory specificity. In this instance, the predator is *Evarcha culicivora* Wesolowska & Jackson 2003, a salticid that feeds especially often on female mosquitoes in the field (Wesolowska & Jackson 2003). Here we consider the specificity of the salticid's predatory behavior for a particular mosquito genus, *Anopheles*. *Evarcha culicivora* is known only from the vicinity of Lake Victoria in Kenya and Uganda. Its typical habitat is tree trunks and walls of buildings. When quiescent, it hides in the grass or in other vegetation close to the ground, but feeding individuals venture into more exposed locations, such as the inside walls of mosquito-infested houses.

In preliminary observations, we noticed that the small juveniles, but not the large individuals, of *Evarcha culicivora* appeared to

be influenced by the mosquito's posture. In particular, *Anopheles* is a mosquito genus known for its distinctive resting posture (Clements 1999): hind legs raised; abdomen angled up at about 45° from the surface on which the mosquito is standing; abdomen and proboscis form a straight line. This posture contrasts with the posture seen in other mosquito species. For example, in *Culex* spp., the abdomen is held parallel to the substrate and the head is tilted ventrally.

Larger individuals of *Evarcha culicivora* typically oriented towards the mosquito, regardless of its posture, and then adopted the type of prey-capture sequence that is typical of many salticid species (see Forster 1977, 1982; Richman & Jackson 1992), making a slow, direct approach, with its body lowered, pausing when close, fastening a dragline and then leaping onto the mosquito. However, when the salticid was a small juvenile of *E. culicivora* and the mosquito was an individual of *Anopheles*, approach was often by way of a detour that ended with the salticid moving in from behind, walking beneath the mosquito's elevated abdomen, and attacking from underneath.

If small juveniles of *Evarcha culicivora* grabbed hold of the dorsal thorax of *Culex*, and the attacked mosquito often flew away, then when the *Culex* took flight, the small juvenile would often lose its grip and fall off. However, when the small juvenile grabbed hold of *Anopheles*' ventral thorax, it generally would hold on when the mosquito took flight, with the mosquito soon succumbing and dropping to the ground, with the salticid on board (Fig. 1).

Here we investigate three hypotheses suggested by these preliminary observations: (1) the small juveniles, but not the larger individuals, of *Evarcha culicivora* adopt an innate *Anopheles*-specific capture tactic; (2) small juveniles use the characteristic rest posture of *Anopheles* as a primary *Anopheles*-identification cue; (3) their *Anopheles*-specific tactic enables the small *E. culicivora* juveniles to be especially effective at capturing *Anopheles*.

## METHODS

**General.**—All testing was carried out between 0700 and 1900 h (laboratory photoperiod 12L:12D, lights on at 0700) at the Thomas Odhiambo Campus (Mbita Point) of the



Figure 1.—Small juvenile of *Evarcha culicivora* feeding on female mosquito (*Anopheles gambiae*). After attacking by grabbing hold of mosquito's posterior ventral thorax from underneath, the salticid has now shifted to feeding from the side of mosquito's thorax.

International Centre of Insect Physiology and Ecology (ICIPE) in Kenya. The elevation of the campus at Mbita Point is 1200 m above sea level (0°25'S–0°30'S by 34°10'E–35°15'E), with 900 mm of rainfall per annum and mean annual temperature of 27 °C. The salticids came from laboratory cultures (for standard salticid-laboratory procedures see Jackson & Hallas 1986). The salticids' rearing environments were 'enriched' (spacious cages, meshworks of twigs within each cage) in a manner comparable to that described by Carducci & Jakob (2000). Maintenance diet consisted of letting each salticid feed to satiation three times per week (Monday, Wednesday, Friday) on midges (Chaoboridae & Chironomidae) collected locally at Mbita Point as needed (i.e. the salticids had no prior experience with mosquitoes of any kind).

For testing, we used adult females of two mosquito species, *Culex quinquefasciatus* Say 1823 and *Anopheles gambiae sensu stricto* Giles 1902. Body length of all mosquitoes used for testing (measured from the head's anterior end to the abdomen's posterior end, ignoring proboscis and ovipositor) was 4.5 mm (matched to the nearest 0.5 mm). Procedures for culturing *A. gambiae* were as described elsewhere (Gougana et al. 2004), and the cultures that we used were initiated from specimens collected at Mbita Point. Specimens of *C. quinquefasciatus* were collected as larvae



at Mbita Point and maintained in buckets filled with lake water in the laboratory until the adults emerged.

Two size classes (matched to the nearest 0.5 mm) of *Evarcha culicivora* juveniles were used: 'small' (body length 1.5 mm) and 'large' (body length 3.5 mm). The small juveniles were individuals that had emerged from their brood sacs 5 days before testing and had not been fed. The large juveniles were kept without prey for 7 days before testing. The 5-day pre-test period was adopted with small juveniles because preliminary trials showed that recent hatchlings became noticeably weak after more than 6 days without food. The 7-day pre-test period was adopted for large juveniles because preliminary trials showed that most individuals respond to live prey and to lures after a fast of this length. No individual of *E. culicivora* and no individual lure was used in more than one test.

Data were analyzed using chi-square tests of independence, with Bonferroni adjustments when multiple comparisons were made (Sokal & Rohlf 1995). Voucher specimens of *Evarcha culicivora* have been deposited at the Museum of Natural History (Wrocław University, Poland), the National Museums of Kenya (Nairobi) and the Florida State Collection of Arthropods (Gainesville, Florida). Voucher specimens of insects have been deposited at the ICIPE Taxonomy Laboratory and at the Florida State Collection of Arthropods.

**Testing whether posture of the prey influenced the decision by *Evarcha* to adopt *Anopheles*-specific capture behavior.**—Four lure types were made, two from using each of the two mosquito species, with each species being in one of two postures (the resting posture typical of *Culex* or the resting posture typical of *Anopheles*). Each lure was made by immobilizing a mosquito with CO<sub>2</sub> and then placing it in 80% EtOH for 60 min. The mosquito was then mounted on the center of one side of a disc-shaped piece of cork (diameter 1.25 X the body length of the mosquito; thickness 2 mm). For preservation, the lure and the cork were next sprayed with a transparent aerosol plastic adhesive and left to air out for at least 24 h before being used.

All mosquitoes had been given blood 4–5 h before being immobilized and used for making lures. Previous work (unpubl. data) with *E. culicivora* has shown that all instars of

these salticids choose blood-fed mosquitoes when the alternative is mosquitoes that have not fed on blood. Each individual of *E. culicivora* used for testing was assigned at random to one of four groups defined by mosquito species and posture, with the proviso that the number for each group was the same ( $n = 50$ ).

Apparatus and testing procedures were similar to those detailed elsewhere (Li et al. 1996; Harland & Jackson 2000) except for modifications that facilitated testing small juvenile salticids. The apparatus was a wooden ramp (15 mm thick, 40 mm wide, 140 mm long) that, with the support of a wooden dowel (15 mm thick), angled up at 20°. The ramp and supporting dowel were on a wooden base (50 mm wide, 150 mm long, 15 mm thick). A lure was positioned at the top of the ramp, in front of a wall which served as a background against which salticids could see the lure. The wall was a piece of brown wood (55 mm high, 40 mm wide, 15 mm thick) glued perpendicular to the top end of the ramp. The lure was centered on the ramp 15 mm from the base of the wall, leaving 10 mm between the wall and the top edge of the cork disc. The lure was positioned so that it faced 45° away from forward (i.e. for *E. culicivora* walking directly up the ramp, the lure was facing 45° to the left or the right). For each lure, whether it was faced left or right was decided a random.

Before testing began, the salticid was kept in a covered pit (diameter 30 mm, depth 10 mm) drilled into the top surface of the ramp (equidistant from left and right side of ramp). The center of the pit was 50 mm from the bottom edge of the ramp (i.e. the lure was positioned 40 mm from the top end of the pit). Tests were allowed to start by removing a transparent glass plate used as a cover. After uncovering the pit, tests were aborted if the salticid failed to come out within 30 min or came out, but then moved off the ramp without first moving toward the lure. In successful tests, the salticid came out of the pit within 30 min after the cover was removed, walked up the ramp and, before 30 min elapsed after leaving the pit, contacted the cork disc or the mosquito, or both. The data we recorded were the salticid's horizontal orientation to the lure and the path it took to reach the lure.

Horizontal orientation of the salticid when approaching the lure was defined as follows:

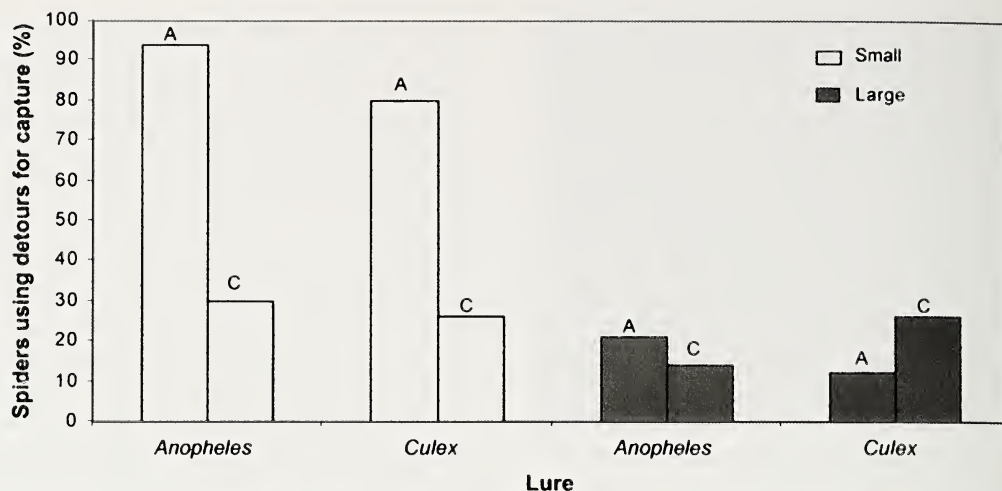


Figure 2.—Percentage of test spiders (juveniles of *E. culicivora*) that made detours when approaching lure (dead mosquito female mounted on cork disc). Two size classes of *E. culicivora* were used: small (body length 1.5 mm) and large (3.5 mm). Four groups of spiders tested, each group defined by mosquito species and posture used for lures: *Anopheles gambiae* in *Anopheles* posture (A), *A. gambiae* in *Culex* posture (C), *Culex quinquefasciatus* in *Anopheles* posture (A) and *C. quinquefasciatus* in *Culex* posture (C). For each bar,  $n = 50$  (no individual of *E. culicivora* and no individual lure used more than once).

front (no more than 45° to the left or the right of the anterior end of the sagittal plane of the mosquito's head); rear (no more than 45° to the left or the right of the posterior end of the sagittal plane of the mosquito's abdomen); side (between front and rear). "Detours" were defined as instances of salticids approaching the lure from the rear or else approaching the lure from the side in the first instance and then moving around to the rear. "Did not detour" was defined as instances of salticids approaching the lure from the front or approaching from the side without shifting to the rear.

**Testing for prey-capture success.**—Large and small juveniles of *Evarcha culicivora* were tested. In each test, one *E. culicivora* juvenile was put inside a clear Plexiglas box (300 mm X 300 mm X 300 mm) with one mosquito (one *Anopheles* or one *Culex* that had had a blood meal 4–5 h earlier). Observations were terminated after the salticid captured the mosquito or 30 min after the test elapsed without the salticid capturing the mosquito.

## RESULTS

**Testing whether posture of the prey influenced the decision by *Evarcha* to adopt *Anopheles*-specific capture behavior.**—When the lures were made from *Anopheles*,

significantly more small juveniles ( $\chi^2 = 43.46$ ,  $P < 0.001$ ,  $df = 1$ ,  $n = 100$ ), but not large juveniles ( $\chi^2 = 0.64$ ,  $P = 0.42$ ,  $df = 1$ ,  $n = 100$ ), of *Evarcha culicivora* made detours when the lure was in the *Anopheles* resting posture rather than in the *Culex* resting posture (Fig. 2). Likewise, when the lures were made from *Culex*, significantly more small juveniles ( $\chi^2 = 29.27$ ,  $P < 0.001$ ,  $df = 1$ ,  $n = 100$ ), but not large juveniles ( $\chi^2 = 0.09$ ,  $P = 0.77$ ,  $df = 1$ ,  $n = 100$ ), of *E. culicivora* made detours when the lure was in the *Anopheles* resting posture rather than in the *Culex* resting posture.

Small juveniles significantly more (Fig. 2) often than large juveniles of *Evarcha culicivora* made detours when approaching *Anopheles* that were in the *Anopheles* resting posture ( $\chi^2 = 55.85$ ,  $P < 0.001$ ,  $n = 100$ ) and *Culex* that were in the *Anopheles* posture ( $\chi^2 = 46.54$ ,  $P < 0.001$ ,  $n = 100$ ). However, the numbers of small and large juveniles of *E. culicivora* that made detours when approaching *Anopheles* in the *Culex* posture ( $\chi^2 = 3.73$ ,  $P = 0.05$ ,  $n = 100$ ) (Fig. 2) and *Culex* in the *Culex* posture ( $\chi^2 = 2.25$ ,  $P = 0.13$ ,  $n = 100$ ) were not significantly different.

**Prey-capture success.**—Large and small juveniles of *Evarcha culicivora* had greater



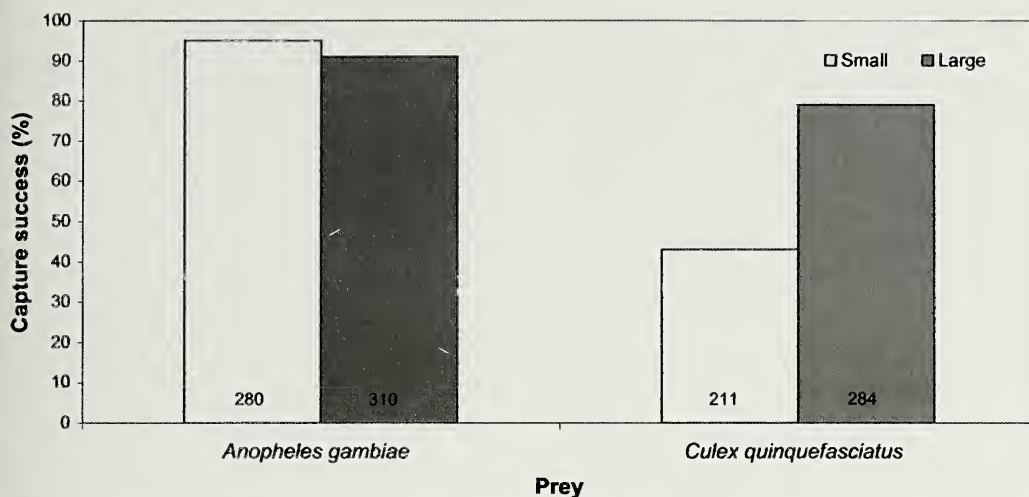


Figure 3.—Percentage of test spiders (juveniles of *Evarcha culicivora*) that captured *Anopheles gambiae* and *Culex quinquefasciatus* in 30 min test (one spider and one mosquito put together in plexiglas box). N is indicated with each bar (no individual of *E. culicivora* and no individual mosquito used more than once). Two size classes of *E. culicivora*: small (body length 1.5 mm) and large (3.5 mm) (assigned at random to test with one or the other mosquito species).

success at capturing *Anopheles* than *Culex* (small,  $\chi^2 = 163.16$ ,  $P < 0.001$ ,  $n = 491$ ; large,  $\chi^2 = 17.78$ ,  $P < 0.001$ ,  $n = 594$ ) (Fig. 3). Small juveniles were less successful than large juveniles at capturing *Culex* ( $\chi^2 = 63.94$ ,  $P < 0.001$ ,  $n = 495$ ), but large and small juveniles had similar success at capturing *Anopheles* ( $\chi^2 = 4.13$ , NS with Bonferroni adjustment,  $df = 1$ ,  $n = 590$ ).

#### DISCUSSION

The distinctive resting posture of *Anopheles* appears to increase the vulnerability of these mosquitoes to predation by the small juveniles of *E. culicivora*. As shown by their response to our experiments with lures and despite their minute eyes, these small salticids can apparently identify the stationary mosquito's posture by sight alone. Having identified the mosquito's posture, a small *E. culicivora* juvenile usually makes a detour that enables it to move under *Anopheles'* raised abdomen from behind. The posture of *Culex* does not afford the small juvenile with comparable easy access to the underside of the mosquito and, upon seeing a mosquito in the *Culex* posture, small *E. culicivora* juveniles usually do not make detours. Evidently, small *E. culicivora* juveniles have evolved fine-tuned innate tactics for predation on *Anopheles*.

That *Anopheles* is generally an easier mos-

quito than *Culex* for *Evarcha culicivora* to overpower is suggested by how both the large and the small juveniles of *E. culicivora* had greater success capturing *Anopheles* than *Culex*. Furthermore, the limited strength of small juveniles is suggested by the finding that small juveniles were considerably less successful at capturing *Culex* than large juveniles, yet they were not less successful at capturing *Anopheles*. Evidently, the *Anopheles*-specific tactic of small juveniles compensates for these spiders' small size, enabling them to be as effective as the larger juveniles when the prey is *Anopheles*. Large juveniles, being more capable of overpowering the mosquito, usually take direct routes. This way they can quickly attack the mosquito, foregoing the lengthier detours adopted by small juveniles.

Although *Evarcha culicivora* appears to be, along with examples from the myrmecophagic (Jackson & van Olphen 1991, 1992; Jackson & Wilcox 1993b; Jackson et al. 1998; Li & Jackson 1996a; Li et al. 1996; Li et al. 1999; Jackson & Li 2001) and the araneophagic salticids (Li & Jackson 1996b; Li et al. 1997; Jackson & Li 1998; Jackson 2000; Harland & Jackson 2001; Cerveira et al. 2003), a species that adopts distinctive prey-specific prey-capture behavior, *E. culicivora* seems to target a considerably different kind of prey. It is easy

to appreciate how ants (Gillespie & Reimer 1993; Vieira & Hoefer 1994; Halaj et al. 1997; Nelson et al. 2004) and spiders (Foelix 1996; Persons & Rypstra 2000; Barnes et al. 2002) can be dangerous prey for a salticid, as they have weapons, such as strong mandibles, strong chelicerae and venom, with which they can seriously, sometimes fatally, injure a salticid. However, mosquitoes appear to have no comparable weaponry with which to confront a salticid.

Risk may be relevant when a mosquito flies away, with a salticid on board, because the salticid loses control over where it might be tossed. Landing in water or in a spider web, for example, might put a salticid in harm's way. However, in the evolution of *Evarcha culicivora*'s prey-specific behavior, the risk of losing a meal may have outweighed these potential risks to life and limb. By attacking from underneath, the small juveniles of *E. culicivora* appear to minimize this risk of being thrown off by the mosquito in flight because they can hold on especially well after an attack from underneath. Another way in which *Anopheles*' posture may be important is by affording small juveniles of *E. culicivora* with the means of getting close without alerting a mosquito (i.e. it would be difficult for *E. culicivora* to move under *Culex* without first bumping into one of the mosquito's legs).

Although it is known that spiders rely to a considerable extent on learned behavior (e.g., Grunbaum 1927; Bays 1962; Edwards & Jackson 1994; Punzo 2004), our methods ruled out prior experience with mosquitoes (i.e. the individuals used in this study had either not been fed at all, or fed on midges alone before testing). Evidently, an innate *Anopheles*-specific tactic (taking a detour and attacking the mosquito from behind and underneath) is triggered when *E. culicivora* sees a mosquito in the *Anopheles* posture. This innate tactic appears to be specific to a remarkably precise prey category, female mosquitoes from one particular genus.

This study demonstrates another unusual example of prey-specific behavior in a salticid. Unlike the better-known examples of pronounced prey-specific prey-capture behavior in myrmecophagic and araneophagic salticids, *E. culicivora*'s *Anopheles*-specific tactic appears to be expressed by only the smaller juveniles.

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## EGG SAC STRUCTURE OF *ZYGIELLA X-NOTATA* (ARACHNIDA, ARANEIDAE)

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**ABSTRACT.** A detailed examination of the egg sac of *Zygiella x-notata* (Clerck 1757) revealed its structure, composition and different fibers. All egg sacs were composed of a basic layer, an insulation layer and an outer layer. The insulation layer consisted of two layers of cylindrical (or tubuliform) fibers with different diameters and probably with different mechanical properties. Knowing the complete structure of the egg sac allows us to locate and extract the needed fibers for further research and to observe how the egg sac composition alters in relation to the habitat.

**Keywords:** Cylindrical (tubuliform) fibers, sticky thread, major ampullate fiber, attachment disc, adhesion droplet.

Of all natural fibers, silk is the most promising for bioengineering because of its biological and mechanical properties. Much is already known about the molecular and mechanical properties of dragline silk of *Araneus diadematus* (Clerck 1757) and *Nephila clavipes* (Linnaeus 1767) (Shao et al. 1999; Vollrath 1999; Vollrath et al. 1998; Vollrath & Knight 2001); still, regarding the other spider silks, these properties have not yet been explored, especially the properties of egg sac silk. Egg sac threads can be very useful for biomedical applications, like sutures, cell support and scaffolds (Gellynck et al. 2003; Van Nimmen et al. 2003). Before one can analyze these properties, the morphology of the egg sac must be investigated to locate these fibers. The primitive role of egg sacs is in giving protection against predators and parasites. Furthermore, the egg sac must create a good microclimate for embryological development, hatching and it must protect the spiderlings until they leave the egg sac (Hieber 1985). As observed by De Bakker et al. (2002), there appears to be a big difference in egg sac structure between families. Since egg sac threads are possibly the earliest silk used by spiders, it is clear that a detailed analysis of these structures can contribute to spider phylogeny. Further research on egg sacs of other families

can perhaps determine, in time, the ancestral construction of the egg sac.

In this study, only egg sacs of *Zygiella x-notata* (Clerck 1757) were investigated. *Zygiella x-notata* is iteroparous and females make most egg sacs in late autumn (Western Europe; November–December). The spiderlings emerge around May of the following year. The egg sacs are elliptical and have a white to yellowish brown color. In addition, they have complex airy structures composed of different layers of silk that enclose and protect the eggs (De Bakker et al. 2002). In the present article, a more detailed description of the egg sac of *Z. x-notata* will be given in which its structure, composition and different fibers will become clear. Knowing the complete egg sac structure will allow us to locate and extract the needed fiber types to investigate their usefulness in several biomedical applications, and to investigate the alteration of egg sac composition in relation to the habitat choice of *Z. x-notata*.

### METHODS

Egg sacs ( $n = 20$ ) of *Z. x-notata* were used to analyze their structure and composition. The spiders were collected in Ghent (Belgium) at Coupure Right (lat. 51°5'53", long. 3°71'11"), in the beginning of November ( $\pm$

Table 1.—Types of fibers measured by one spider (*Z. x-notata*).

Type of fiber	Average diameter (μm)	St. Dev.
MA threads		
Basic layer (n = 11)	2.63	0.13
Outer layer (n = 13)	2.41	0.35
Dragline (n = 10)	1.54	0.06
TU fibers		
1st insulation layer (n = 231)	3.29	0.30
2nd insulation layer (n = 324)	3.84	0.24

80 spiders). They were kept in the laboratory in small, round, plastic (PS) cups, with plastic (PVC) lids (diameter: 50mm, height: 25mm). The lids were pierced for aeration and to make them an easier surface for walking. All spiders were fed fruit flies (*Drosophila* sp.). A high level of air humidity was provided by a water-saturated piece of plaster placed on the bottom of the cups. It was moistened every 4 days with a mixture of water and nipagine (Alpha Pharma) to prevent fungal growth. The temperature was kept constant ( $23 \pm 1$  °C) and light was regulated following a constant day-night period (16h–8h). In this way, a high uniformity in egg sac structure was obtained which simplified the observations. Draglines, for comparison, were collected from the spider while she was hanging. Voucher specimens have been deposited in the “Evolutionary Morphology of Vertebrates & Zoology

Museum”, Ghent University in Belgium (UGMD 104091).

The morphological study was performed by means of a stereomicroscope (Wild M5), a light microscope (Olympus CH-2) and a Scanning Electron Microscope (JEOL JSM-5600 LV, SEM). For light microscopy, slides of strands and connections were prepared with glycerine to prevent air bubbles. Photographs taken by the light- and stereomicroscope were made with a camera (Nikon coolpix 900) mounted on the microscope. For the SEM, samples (connections, fiber types) and a completely dried egg sac were mounted on stubs (standard and large (32mm)) and coated with gold (JEOL JFC–1200 Fine coater, 8nm). An image processing system (Lucia System for Image Processing and Analysis version 4.51), made it possible to process and analyze real color photographs, like measuring the thickness of the draglines and egg sac fibers of one egg sac (Table 1). In order to compare the thickness of the egg sac fibers of the first and second insulation layer, a student t-test ( $P = 0.05$ ) was performed supposing a normal distribution of the measurements using the Statistica program (Statsoft 2001 Release 6.0). Terminology, except as defined here, is from earlier studies (Peters & Kovoer 1991; Zschokke 1999, 2000; Benjamin et al. 2002).

RESULTS

All 20 egg sacs were analyzed and a great uniformity in their structure was visible. Figure 1 shows a scheme of this uniform egg sac structure.

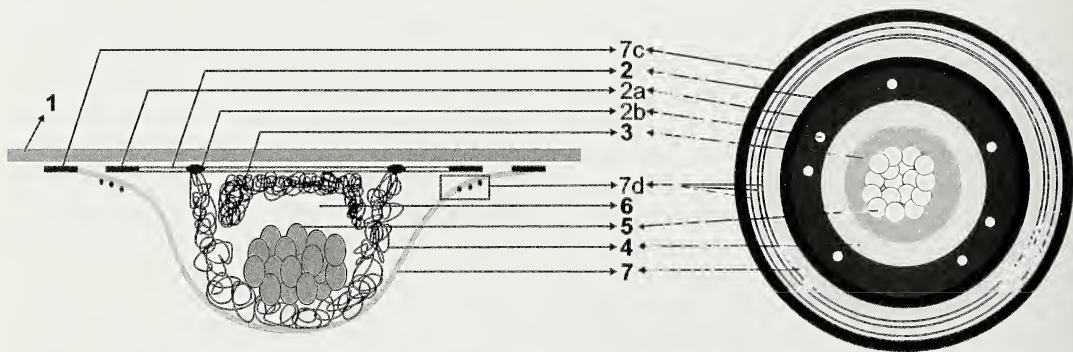


Figure 1.—Older egg sac structure of *Z. x-notata*: Left: side-view; right: top view, most common placement of the different structures. 1 = substrate (lid), 2 = basic layer (a = attachment discs of the basic layer, b = adhesion droplets), 3 = first insulation layer, 4 = second insulation layer, 5 = eggs forming the egg chamber, 6 = egg sac space, 7 = outer layer (c = attachment discs of the outer layer, d = sticky threads).





Figures 2–4.—Basic layer. 2. Basic layer with an attachment of egg sac fibers of the first insulation layer on the left side (stereomicroscope); 3. Basic layer in more detail with some major ampullate (MA-MA) connections (SEM); 4. Two major ampullate (MA) threads of the basic layer (SEM).

**Basic layers.**—When in the cup, the spiders generally walked on the lid (Fig. 1 (1)), and constantly produced draglines (major ampullate (MA) thread), which they fixed on the substrate by means of attachment discs (Fig. 1 (2a)). In this way a parallel, sheet-like layer was formed and was here named the “walk plate”. The MA thread of this layer was always doubled or sometimes fourfold (Figs. 3, 4). Before egg sac construction, an additional network of fibers was fixed on the center of the walk plate, which was here named the “stitch plate” (observed in 7 egg sacs), because it was on this layer the tubuliform (TU) fibers were attached. In contrast with the walk plate, the stitch plate was a tightly woven network that was attached to the substrate by “adhesion droplets” (Fig. 1 (2b)). The threads resembled MA threads such as those of the walk plate but they had a smaller diameter.

**Attachment discs.**—An attachment disc (Fig. 1(2a)) consisted of an MA thread (Fig. 5, a) and a big sheet of finer fibers (= the disc; Fig. 5, b). The dragline was continuous and did not stop in the disc. The area of the disc varied and appeared to depend on the importance of the attachment. The number of attachment discs per basic plate (Fig. 1(2a)) was relatively small according to the number of attachment discs of the outer layer (Fig. 1(7c)).

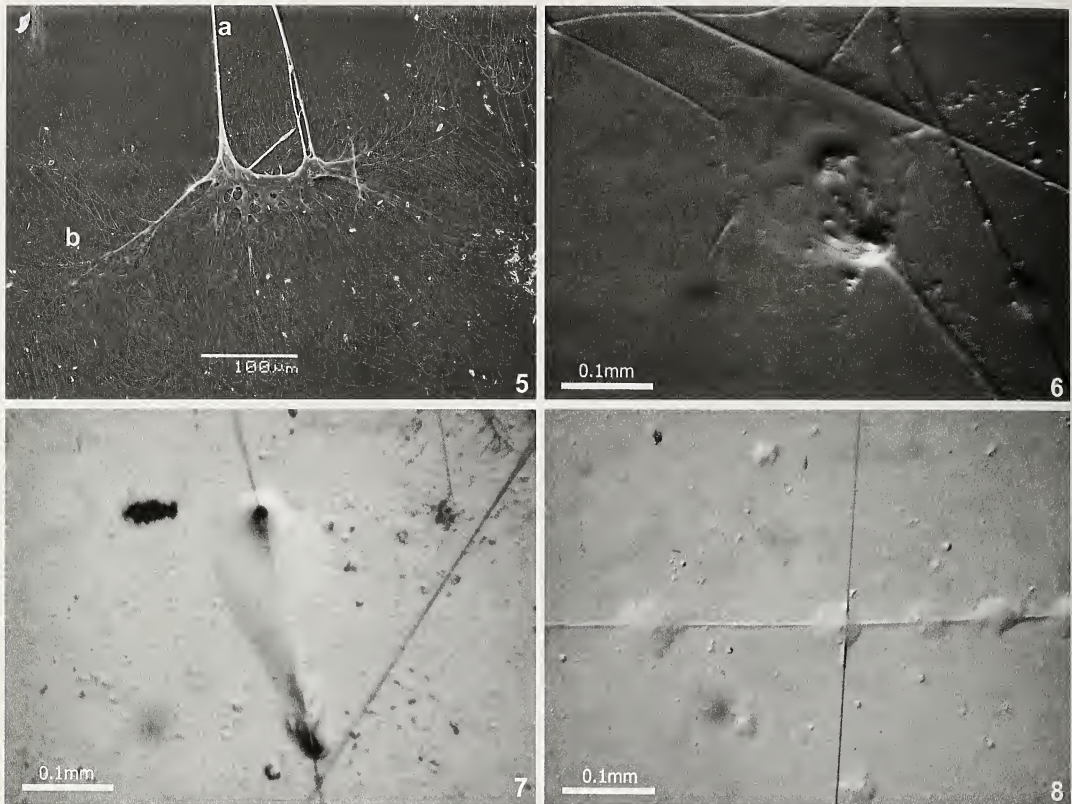
**Adhesion droplets.**—Adhesion droplets (Fig. 1 (2b)) consisted of a glue-like droplet in which a fiber was placed without the presence of a disc (Figs. 7, 8). These attachments were less abundant than attachment discs, they were more centrally placed in the egg sac (Fig. 1(2b)) and seemed to attach the stitch plate to the substrate (observed in seven egg sacs).

Figure 6 shows in detail an ending fiber in an adhesion droplet. The thread was double stranded and once in the droplet, it spread out in many finer fibers. This seemed to be different from the other fibers (Fig. 7, 8) which were only connected to the substrate by means of a glue droplet.

**Major ampullate (MA-MA) thread connection.**—The basic layer contained many fixations between MA threads. These connections could be complex and consisted of thread-like glue secretions (Figs. 9, 10). The secretions enveloped the two MA threads individually and there was a stretch zone present in the secretion between the two MA threads (Fig. 10, a).

**Insulation layer.**—This layer formed the actual egg sac and consisted of TU (tubuliform) fibers (Figs. 11, 12). The insulation layer could be subdivided into two layers: a “first” and a “second” insulation layer. These layers consisted of crisscrossed, tufted fibers with few or no connections (Fig. 11). Sometimes TU fibers were found doubled (Fig. 11, a). They were lying next to each other in close contact, pointing in the same direction and seeming to adhere to one another along a fine line.

TU fibers of the first insulation layer (Figs. 1 (3), 13) were attached to the basic layer (Fig. 2), after which the spider pulled the fibers out of her spinnerets and attached them again to the basic layer a bit further. In this way she spun around attaching the TU fibers, making a cup in which to put the eggs. After the eggs were laid (Fig. 1 (5)), a second insulation layer (Figs. 1 (4), 14) was placed over the eggs and the first insulation layer. This layer was also attached to the basic layer in



Figures 5–8.—Fiber-substrate connections. 5. Attachment disc, a = dragline, b = disc of finer fibers (SEM); 6. One adhesion droplet fixing an ending thread (stereomicroscope); 7. Fixation of a continuous fiber with one glue droplet (stereomicroscope); 8. Fixation of a continuous fiber with several glue droplets (stereomicroscope).

the same way as the first insulation layer, but was more peripheral.

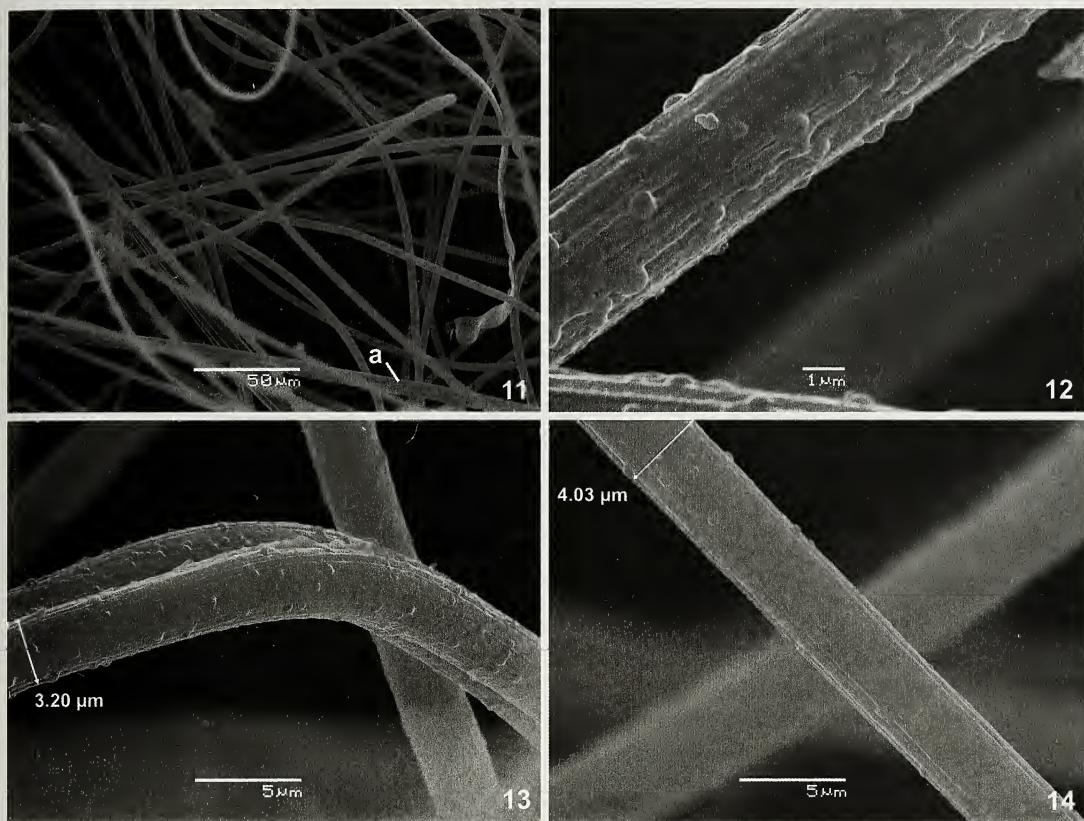
Statistical analysis showed a highly significant difference in thickness between the TU

fibers of the first and the second insulation layer within the same egg sac. ( $df = 230$ ,  $p < 0.0001$ ). The first insulation layer ( $3.29 \mu m \pm 0.30 \mu m$ ) had finer fibers than the second



Figures 9–10.—SEM pictures of a basic layer MA-MA thread connection. 9. Overview of an attachment; 10. In more detail; a = stretch zone in the connecting secretion.





Figures 11–14.—SEM pictures of the insulation layer. 11. Overview of the fibers of the insulation layer, a: doubled TU fiber; 12. Detail of an egg sac fiber; 13. Detail of an egg sac fiber of the first insulation layer; 14. Detail of an egg sac fiber of the second insulation layer.

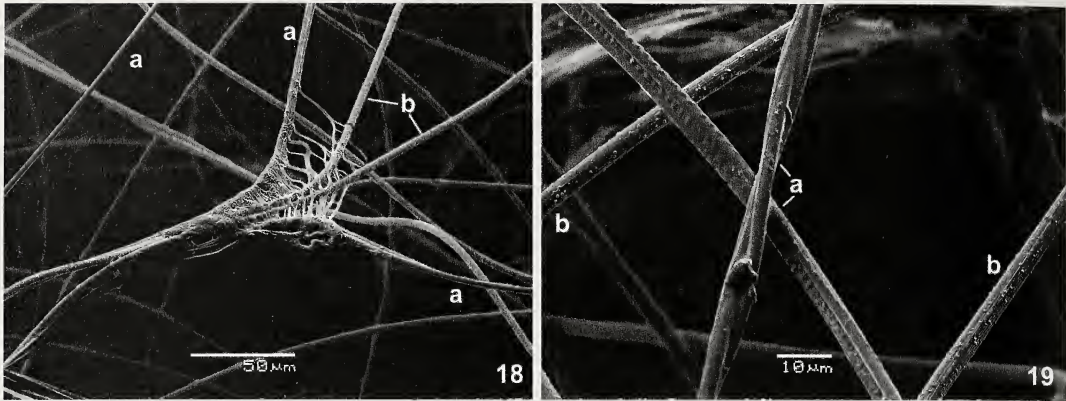
insulation layer ( $3.84 \mu\text{m} \pm 0.24 \mu\text{m}$ ) (Table 1). Although they differed in thickness, they did not differ in surface structure and appearance (Figs. 13, 14). Egg sac fibers of the first and second insulation layer were connected to the basic layer in the same way (Fig. 15, 16). These connections consisted of four to six

continuing TU fibers (Fig. 17, a) attached together with a kind of glue to one MA thread (Fig. 17, b) of the basic layer.

**Egg sac chamber.**—In recently placed egg sacs, only fibers surrounding the egg mass (Fig. 1 (5)) were found, and no fibers were found between the eggs. In older egg sacs, a



Figures 15–17.—Egg sac fiber-basic layer connection. 15. Attachment of the first insulation layer to the basic layer (stereomicroscope); 16. Multiple egg sac fibers attached at one place on a basic layer thread (MA) (stereomicroscope); 17. Detail of multiple egg sac fibers (a) attached to a basic layer thread (b), somewhat torn apart (SEM).



Figures 18–19.—SEM picture of the outer layer. 18. Attachment of the outer layer thread to some egg sac fibers of the second insulation layer; 19. Detail of some outer layer threads. a = outer layer threads, b = egg sac fibers.

space (Fig. 1 (6)) was found between the eggs and the first insulation layer.

**Outer layer.**—The outer layer (Fig. 1(7)) was placed over the insulation layers and basic layer. It was made up of an airy network of threads attached to the substrate by means of attachment discs (Figs. 1 (7c), 20). These attachment discs were numerous and peripherally situated, forming the edge of the egg sac. They were similar in structure like those found in the basic layer. The threads were doubled and contained a kind of glue on their surface (Fig. 19, a) in contrast to the MA threads of the basic layer (Fig. 4).

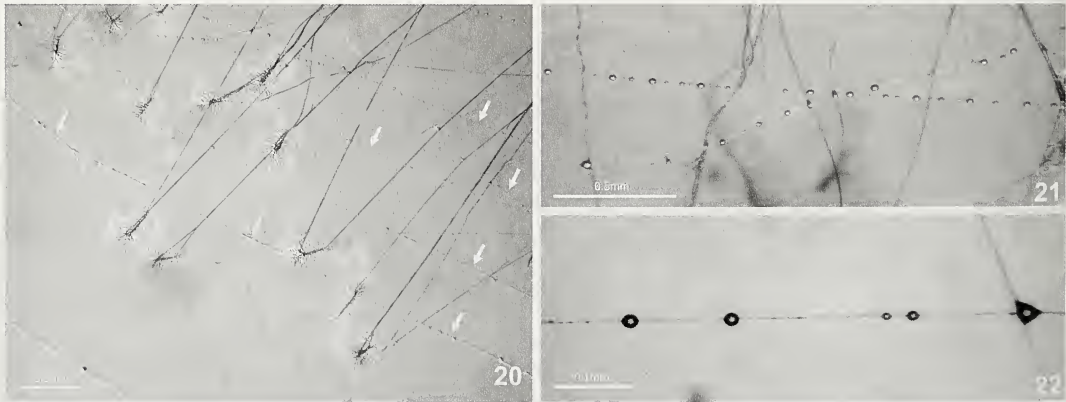
There were also connections found between the fibers of the outer layer (Fig. 18, a) and the second insulation layer (Fig. 18, b). These connections consisted, like MA-MA thread

connections, of a kind of glue and finer fibers (Fig. 18). Although there was much more variation in the number of fibers included in this connection type, there were always two MA fibers (one MA thread), whereas the number of TU fibers was variable.

In five egg sacs, a sticky thread was observed on the outer layer which resembled the sticky threads of orb webs (Figs. 1 (7d), 20–22). The sticky threads were winded several times around the egg sac beginning from the attachment discs of the outer layer, going inwards with an almost constant interval (Fig. 20, arrows).

DISCUSSION

Egg sacs in spiders vary substantially in structure interspecifically but usually display



Figures 20–22.—Stereomicroscope pictures of the outer layer. 20. Outer layer with attachment discs and diagonally on it the sticky threads indicated with arrows; 21. Sticky threads with glue droplets; 22. Detail of the glue droplets.



consistent similarities intraspecifically, that is, most families have egg sacs of only one or two structural types (Austin 1985). The egg sacs of *Zygiella* were fairly uniform and consisted of a basic layer, a double insulation layer and an outer layer. This structural composition is consistent among most spiders belonging to the family Araneidae (unpub. data).

**Basic layer.**—The basic layer is composed of a walk plate and a stitch plate and forms the basis for egg sac construction. The MA threads (draglines) of the walk plate are stronger and stiffer than TU fibers (Van Nimmen et al. 2003). Their presence in the basic layer and the outer layer is probably to fix the egg sac well to the substrate and to support the egg mass. The fact that the fibers of the stitch plate look like MA threads and have a smaller diameter suggests that they originate from the minor ampullate (MI) glands. The stitch plate is probably present in all egg sacs but due to the difficult observation of these fibers it was only detected in seven egg sacs.

In nature however, one can sometimes observe that a new, fresh egg sac is attached to an older one. In this case it can be expected that the “outer layer” of the older egg sac serves as a basic layer for the new one what costs the spider less energy.

**Attachment discs.**—It is known that the piriform spools (Pi) produce the disc while the MA thread (dragline) is extruded by the MA spigots on the anterior spinnerets (Foelix 1996). The attachment discs used for the basic and outer layer strongly resemble those used for walking and web building described by Schütt (1996), so it is not so surprising that they are used for the egg sac construction as well.

**Adhesion droplets.**—These adhesion droplets were no artifacts of oviposition, because no “glue droplets” were observed without fibers and the fixation of the fibers to the substrate was too specific. We suggest that the MI fibers of the stitch plate are fixed to the substrate in this way. The Pi spools are probably not involved in this fixation type because the MI spigots are located too far from them. A glue spool/spigot located closer to the MI spigot is more likely.

We hypothesize that the ending thread seen in Fig. 6 does probably not originate from the minor ampullate spigots but rather from the

MA spigot and that it is the beginning or ending of an MA thread, which would explain their low abundance.

**Major ampullate (MA-MA) thread connection.**—The thread-like glue secretions make us suspect that these connections originate from the Pi spools of the anterior spinnerets, like the attachment discs. Most of the connections and supporting structures in araneoid webs are also made up of attachment discs: sticky spiral thread to radius, auxiliary spiral to radius, radius to frame and some connections to the hub (Peters & Kooor 1991; Peters 1993; Benjamin et al. 2002). The stretch zone indicates that the fibers were laid parallel while fixing and reorientated afterwards.

**Insulation layer.**—*Zygiella x-notata* simultaneously produces six TU fibers by six TU spigots, two on the median spinnerets and four on the posterior spinnerets (Foradori et al. 2002), forming the two insulation layers in the egg sac. Measuring the thickness of the fibers of the two insulation layers was only executed on one egg sac but recent experiments (unpub. data) indicate that the found difference in thickness is generally applicable. The difference in thickness between the fibers of the two layers is most likely due to the difference in volume of the TU glands before and after placing the eggs. Before oviposition, the glands are limited in space for expansion. Probably a smaller lumen is causing a smaller secretion which results in a finer fiber of the first insulation layer. After oviposition, more space is available in the abdomen causing a bigger lumen and secretion, resulting in a thicker fiber of the second insulation layer. This difference in diameter will probably also be reflected in the mechanical properties of these fibers.

MA and TU fibers from *Z. x-notata* are morphologically very different. MA fibers have a smaller diameter (Table 1) and no underlying structures (Fig. 4), unlike TU fibers (Fig. 12) (Van Nimmen et al. 2003). The fact that TU fibers are another type of fiber means that they have some advantages compared to MA fibers: 1. In water, TU fibers only increase in diameter without longitudinal shortening (pers. obs.), unlike draglines which supercontract (Bell et al. 2002). This observation suggests that TU fibers can play a role in moisture regulation in the egg sac. This would also con-



firm the suggestion of Hieber that TU fibers can serve as a regulator of the relative humidity by taking up water if the relative humidity is too high and releasing water if it is too low. It would also explain why fibers of the second insulation layer are thicker than the first, because the second insulation forms the actual barrier with the environment. 2. The fact that TU fibers do not supercontract is probably also favorable for the survival of the eggs. If TU fibers should supercontract, the eggs would probably be killed if egg sacs are placed in humid environments. 3. It has been suggested that the egg sacs of *N. clavipes* protect the egg mass against micro-organisms (Austin 1985). Like sticky threads, it is possible that TU fibers possess a high concentration of potassium dihydrogen phosphate to prevent the eggs from bacterial and fungal degradation (Schildknecht et al. 1972). 4. The tufted nature of egg sac fibers protects the eggs against mechanical damage, predation or parasitism (Guarisco 2001) and can also save the eggs and spiderlings from drowning and physical damage (Hieber 1992a, b).

Egg sac fibers are always attached to the threads of the basic layer or, in nature, the MA threads of webs or the outer layer of egg sacs and never to the substrate. Apparently they can only be attached to other fibers. The TU fibers (of the two layers) are also attached to other fibers with glue-like fibers, which includes both. The origin of these secretions is however unknown.

**Egg sac chamber.**—In recently placed egg sacs, the eggs are encircled by the first and second insulation layer which forms the egg chamber (Fig. 1 (5)), which is here the same as the egg sac chamber. By older egg sacs however, the mass of the eggs and the upside-down position (horizontal or vertical) causes the egg sac to sag out due to gravity, forming a space (Fig. 1 (6)) between the eggs and the first insulation layer. So here the egg sac chamber is the total of the “egg chamber” (Fig. 1 (5)) and the “egg sac space” (Fig. 1 (6)). It is possible that this egg sac space is vital for the hatching and the survival of the young spiderlings till the first ecdysis.

**Outer layer.**—The threads of the outer layer are double stranded, attached to the substrate with attachment discs and have a similar morphology like draglines. All these observations suggest that these threads originate from

the MA spigots. If the MA threads used for the egg sac are compared with the dragline of the same spider, a remarkable difference ( $\approx 1\mu\text{m}$ ) in thickness can be seen (Table 1). Because both fibers are from MA gland origin, this difference can only be explained by the way they were produced. As found by Vollrath et al. (2001), both thread extension and reeling speed affect the diameter of the thread by a constant temperature. Draglines in this experiment were collected from hanging spiders which resulted in a bigger thread extension as well as a higher reeling speed resulting in a fine thread. Threads used for the egg sac structure are never stretched in this way because the spider is at all time attached to the substrate with her legs and the reeling speed was like the walking speed of the spider, resulting in a thicker thread. The difference in thickness between the fibers of the basic layer and the outer layer (Table 1) is probably due to a greater thread extension in the fibers of the outer layer caused by a bigger load on the thread from the mass of the spider. The connections of the outer layer threads to the second insulation layer fibers have probably the same origin as the MA-MA thread connections.

In contrast with *A. aurantia*, the outer layer of *Z. x-notata* is not as dense, which would suggest that it is rarely or never attacked by generalist predators. This, however, is not so. These egg sacs were protected against predators by use of a defensive layer made up of sticky threads. These sticky threads were only found on the outer layer of the egg sac in a very specific arrangement. It is very likely that these sticky threads are the same sticky thread as those used in the sticky spiral of webs and that they fulfill the same function. The fact that *Z. x-notata* is iteroparous means that she can replace the sticky thread of the egg sac when it dries out. This sticky thread was only observed in five egg sacs where mites were present in the cup, which may explain the extra security in contrast with the other observed egg sacs.

In conclusion, egg sacs are built of four layers; a basic layer, a first insulation layer, a second insulation layer and an outer layer. This study shows for the first time the details of the different fibers involved in the egg sac, their possible function, their connection types and the role of the different structures they form in the egg sac. The basic- and outer layer are



formed of MA threads which are for support and attachment of the TU fibers. In contrast, the insulation layers are made up by TU fibers and arranged in two layers. The fibers of the first insulation layer are finer than those of the second insulation layer which could indicate that the second insulation layers has a moisture regulation function in the egg sac. In some egg sacs there was an additional fiber type present, namely sticky threads. These sticky threads were found on the outer layer and probably protect the egg sac against generalist predators, such as mites.

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## NOTES ON THE NATURAL HISTORY OF A TRAPDOOR SPIDER *ANCYLOTRYPA* SIMON (ARANEAE, CYRTAUCHENIIDAE) THAT CONSTRUCTS A SPHERICAL BURROW PLUG

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**ABSTRACT.** Burrows of an unidentified species of *Ancylotrypa* Simon from the floodplain of the Nyl River in Limpopo Province, South Africa are described. In addition to constructing a thin trapdoor, members of this species construct a hard, spherical plug or marble from soil particles held together with silk. Burrow structure, the plug and associated behavior are described for the first time.

**Keywords:** Marble spiders, burrows, spherical plug, trapdoor, *Ancylotrypa*

The genus *Ancylotrypa* Simon 1889 contains 48 species 32 of which occur in southern Africa (Dippenaar-Schoeman 2002). Members of this genus construct and occupy silk-lined burrows that vary from simple, single-tube structures to Y or U shaped configurations or burrows with multiple arms, not all of which necessarily reach the soil surface. Various forms of soft lids close the burrow entrances (e.g., Dippenaar-Schoeman 2002: p.43 fig. 26). Although burrows of several species of *Ancylotrypa* have previously been described, this is the first species to be shown to construct a spherical plug or “marble” which is used to close and possibly protect the burrow.

This study was conducted on the floodplain of the Nyl River (24°39'S: 28°42'E) in the Limpopo Province of South Africa at Nylsvley Nature Reserve from the summer of 1992–1993 through 2002–2003. The floodplain is usually inundated during the southern summer (November–March) but in years of poor rainfall the area remains entirely dry. When several years of exceptionally high rainfall occur it may remain inundated for more than one season (Barnes et al. in press).

In the late 1980s we observed colonies of trap door burrows in the sodic alluvial soils of the Nyl River floodplain. Small spheres made of tight packed sand resembling tiny marbles of various sizes were noted lying on the ground in the vicinity of the colonies but the connection between these marbles and the spiders that produce them was not made until 1992–1993 when burrows were examined in detail.

Burrows were excavated at different times of the year: during dry and wet seasons and in years of average, low and high rainfall. A colony would be located, the ground swept with a hard floor brush and a burrow chosen for excavation. Burrow lids

were gently scratched to ascertain which were occupied and it was found that if spiders were present, they would tug at the lids which, because they are soft, made them cave inwards. If the lids were scratched too hard, movement would cease and it was assumed the spider had retreated lower into its burrow. A hole was dug vertically about 60 mm distant from the chosen burrow lid to a depth of about 200 mm at what was hoped to be more or less parallel to the burrow and the hard soil between the initial hole and the burrow was removed. Once the main arm of a burrow was located even more careful digging was carried out to find the direction of the side arm until the whole burrow was located. The burrow was measured and only then would the burrow wall be breached below the junction of the arms and subsequently sectioned from the bottom towards the top. Burrow shape, the spider, any young or eggsacs, prey remains and the position of the spherical plug were noted. Some plugs were cut open to see how they were constructed.

All the burrows ( $n = 97$ ; Table 1) excavated were roughly Y-shaped with two short arms forming a V above the junction of the main burrow (Figs. 1 & 2). The angle of the burrow to the soil surface varied between about 50° and 60° and all burrows had lids (Table 2). The largest burrows were those of adult females, generally about 150 mm deep: one arm between 30 and 40 mm long from the junction to the surface of the soil, ending in a cuff and wafer-lid trapdoor, the other ending some 10 mm below the soil surface. The trapdoor was soft, folded and asymmetrical. Larger burrows had lids with a raised “cuff” (Leroy & Leroy 2000) of silk around the lid as well as the trapdoor and were found to contain adult female spiders. All the burrows excavated contained hard, spherical plugs or “marbles” formed of soil particles bound together by



Table 1.—Total number of burrows of *Ancylotrypa* sp. excavated over a ten year period from 1992–2002 including number of burrows containing young or eggsacs. Immature spiders were less than 8 mm in length. No adult males were found in burrows.

Month	Egg		No young or egg		Imma- ture	Total
	Young present	sacs present	sacs present	sacs present		
Jan.	3	2	—	—	2	7
Feb.	4	2	—	—	3	9
Mar.	4	2	—	—	4	10
April	3	1	—	—	5	9
May	3	2	1	1	4	10
June	1	2	—	—	4	7
July	1	2	2	2	2	7
Aug.	1	1	1	1	3	6
Sept.	2	1	1	1	2	6
Oct.	2	1	1	1	3	7
Nov.	2	1	2	2	4	8
Dec.	3	1	—	—	6	11
Total	29	18	8	8	42	97

fine, strong silk. The size of the marble corresponded closely to the burrow diameter. On cutting open the spherical marbles, all were found to contain only soil particles and no prey remains. Many marbles of different diameters were found on the surface of the soil and it seems that the spiders periodically construct new ones, probably as they grow and enlarge their burrows the spiders discard the old, smaller marbles (Fig. 3). During nocturnal observation, the spiders were found to be sit-and-wait predators. They do not leave their burrows to hunt but lurk below the trapdoor for prey to come close enough to be snatched and taken down into the burrow. On excavating the burrows, if the spider was undisturbed, the marble would be found at the top of the shorter, blind arm. Likewise, if during excavation, the spider retreated to the bottom of the burrow, the marble would still be at the top of the shorter arm. However, if the burrow wall was carefully breached for observation and if the trapdoor was then scratched, the spider would pull on the door presumably to test what the disturbance was. More vigorous scratching, which eventually broke the door, sent the spider scurrying from the open arm into the blind one, where it retrieved the marble (Fig. 4) and then positioned the marble below the door, hiding below it.

All the burrows excavated housed female or immature spiders and those of adult females also contained eggsacs or young at all times of year. No adult males were collected from burrows. Prey remains and exuvia were found to be stored above

the marble at the top of the blind arm while eggsacs were generally suspended from the burrow walls near the bottom of the burrow.

On checking geomorphological and flooding data it became apparent that the area the spiders inhabit does not become inundated when the river floods but because it is rather flat, will be covered in water from a few to several centimeters deep for varying lengths of time after even a single rain storm. Since the first observations in the southern summer of 1992–1993 we have had the opportunity to observe the effect of showers of varying intensity and duration and noted that sheets of water form and, because the soil is virtually impermeable, the humidity penetrates it very slowly indeed. In years of steady rainfall these sheets of water persist all summer, being replenished with each successive shower although if it does not rain regularly the shallower parts dry up after a few days.

The whole area where the spiders are found is interspersed with vegetated “islands” which are up to half a meter higher than the surrounding bare parts. During the summer months there is good grass cover and considerable termite activity. According to Ferrar 1982, 12 species of termites can be found on what he termed “turf vlei” (here called sodic, alluvial soils). Three species are dominant with *Macrotermes natalensis* being the most visible. It was expected that termites would be the main prey for this spider but a cursory examination of prey remains shows small Coleoptera and ants constitute the main prey along with the remains of a few termites and other small unidentifiable hymenopterans.

The population density of this species of *Ancylotrypa* in the study area is very high, especially on slightly raised and sloping ground. A square meter transect was marked out into 200 mm squares on one of these shallow slopes, the covering of loose soil swept from the top few millimeters and 170 burrow lids counted. While excavating burrows, still more were found which had not been apparent from the surface. At a rough estimate, in optimum areas, there could be around 200 burrows per square meter but these did not extend into areas with different soil textures.

There are “Y” shaped burrows constructed by other *Ancylotrypa* species but until this study, there are no records of marbles being constructed by spiders in this genus. The only other similar behavior seems to be that of a trapdoor spider in the family Nemesiidae, *Stanwellia nebulosa*, found in South Australia (Main 1976). This species uses a pebble or stone attached to a sock and stores in a side pocket about halfway down its burrow, counterbalanced to fall neatly so that when it feels threatened it can be pulled down to close off the bottom half of the burrow.

Because the burrows of this species of *Ancylotrypa*



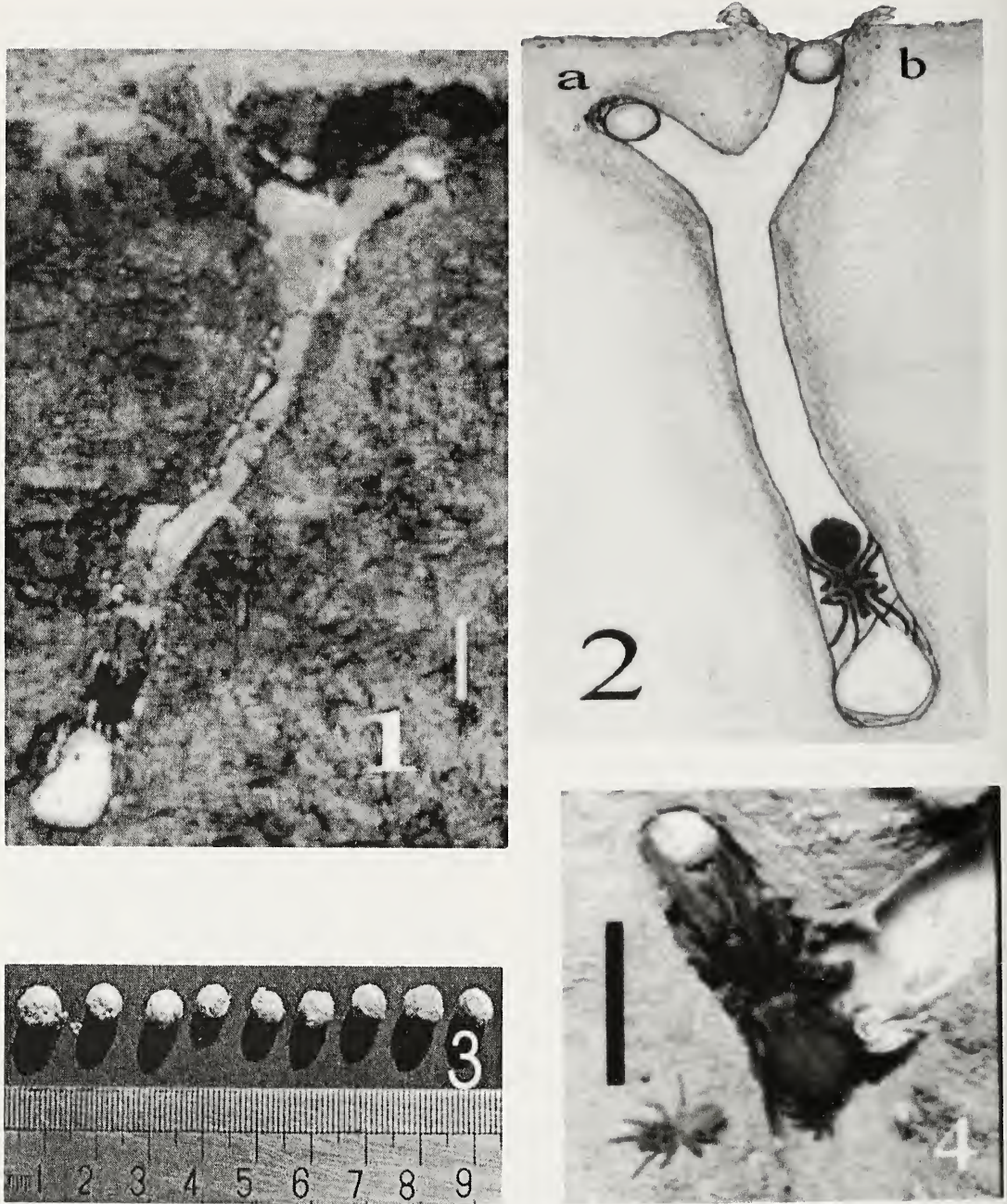


Figure 1.—Excavated burrow of adult female *Acylotrypa* showing marble stored at the top of the blind arm. The spider is just above an egg case which is attached to the wall at the bottom of the burrow. Scale bar = 10mm.

Figure 2.—Diagram of burrow showing the two positions of the marble: (a) stored at the top of the blind arm and (b) in position to plug and protect the burrow.

Figure 3.—Size of marbles shown next to a metric scale.

Figure 4.—Female spider collecting marble from the blind arm preparatory to plugging the open arm of the burrow. Note young still in material burrow, Scale bar = 10 mm.



Table 2.—Numbers and sizes of burrow lids of *Ancylotrypa* sp. measured in 1 square meter area.

Size of burrow lid (diameter in mm)	Number
<2	42
2–4	83
4–6	32
6–8	13

*trypa* are found on slightly sloping ground where water can drain away, it appears that the hypothesis that the marbles are used to stop water flooding the burrow is probably not the case. The conclusion is that the marbles are used by the spider to plug the burrow when the trap door is breached and we suggest a vernacular name of “marble spiders”.

It was not possible to identify the species on which this study is based because the genus *Ancylotrypa* is in need of taxonomic revision. It is tentatively identified as *Ancylotrypa brevipalpis* (Hewitt 1916) described as *Pelmatorycter brevipalpis* and originally placed in the family Ctenizidae by Hewitt based on material collected from Pretoria and from one other locality, Crocodile Bridge. Raven (1985) transferred the genus to the family Cyrtaceniidae and the species to the genus *Ancylotrypa*. If it is *A. brevipalpis*, males have been collected in pit traps and recorded from Gauteng and the North West Provinces of South Africa (Dippenaar Schoeman 2002) which means that Nylsvley Provincial Nature Reserve (24°39’S:28°42’E) and the nearby Mosdene Private Nature Reserve (24°31’S:28 °47’E) in Limpopo Province, South Africa will constitute new locality records. Voucher specimens are deposited in The National Collection of Arachnida, ARC-Plant Protection Research Institute, Pretoria, South Africa (PPRI).

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## THE SPERMATOOZOA OF THE ONE-PALPED SPIDER *TIDARREN ARGO* (ARANEAE, THERIDIIDAE)

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**ABSTRACT.** The species of the genus *Tidarren* are known for their one-palped males and outstanding copulatory behavior. In our ultrastructural observations of *T. argo* Knoflach & van Harten 2001, we show that this species possesses highly specific spermatozoa which differ from those found in other spiders: The nucleus of the sperm cell is strongly elongated and characterized by a conspicuous implantation fossa. The basis of the axoneme is located close to the acrosomal complex. The axoneme starts in front of the implantation fossa which extends deeply into the postcentriolar elongation. The implantation fossa is filled with dense staining globules and granules as in other theridiid species. Apart from these peculiarities, in *T. argo* the proximal centriole is located extraordinarily far away from the distal one. The encapsulated cleistospemia are surrounded by a thin secretion sheath. Remarkably, mature spermatozoa are not densely packed, but embedded in a copious secretion.

**Keywords:** Spider sperm ultrastructure, nucleus, implantation fossa, centriole, secretion

The theridiid spider *Tidarren argo* which was first described by Knoflach & van Harten 2001 from Yemen exhibits several peculiarities in exomorphology and behavior. The males amputate one palp some hours after the penultimate molt. Such self-amputation is known only from *Tidarren* and *Echinotheridion* species, but from no other spider (Knoflach & van Harten 2000, 2001; Knoflach 2002). The reason for palp removal may be to increase locomotor performance as shown for *T. sisypoides* (Walckenaer 1842) (see Ramos et al. 2004). In *T. argo*, the male dies during copulation and even becomes emasculated by the female. Immediately after insertion the fe-

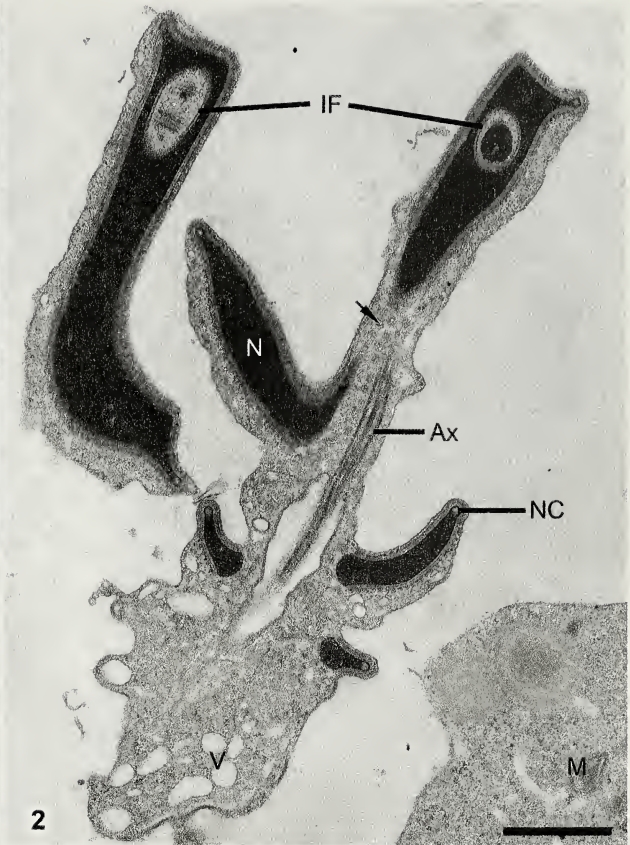
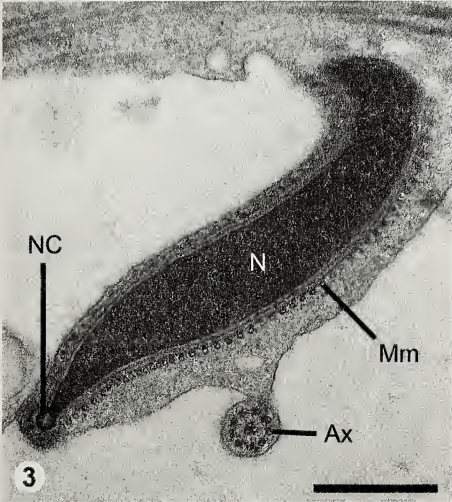
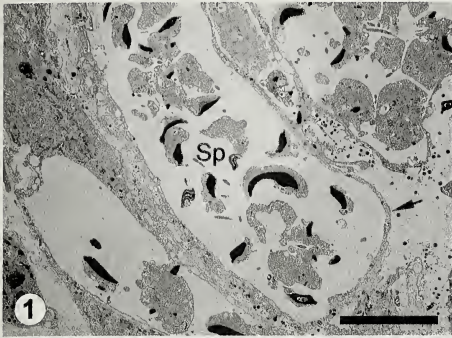
male twists off the single male palp, which then continues with sperm transfer disconnected from the male (for details see Knoflach & van Harten 2001). Based on these outstanding features, the present study focuses on the fine structure of the spermatozoa, which are briefly compared with our own unpublished observations on other theridiid spiders.

*Tidarren argo* from Yemen, Khamis Bani Sa'd, 15°11'N 43°25'E, were kept alive in Innsbruck, in plastic boxes at room temperature. From this breeding stock, male specimens were dissected and fixed in 3.5% glutaraldehyde in 0.1 M phosphate buffer, followed by postfixation in buffered 2% os-

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Figures 1–4.—Late-stage spermatids in *Tidarren argo*. 1. Overview of part of the testis. Spermatids grouped together in cysts which are surrounded by extensions of the somatic cells (arrow). Scale bar = 10  $\mu$ m. 2. Longitudinal section of two spermatids. The ribbon-shaped nucleus coils several times around the axoneme as evident on the right spermatid. Arrow points to nuclear pores. Scale bar = 1  $\mu$ m. 3. The nucleus is surrounded by a manchette of microtubules. Nuclear canal runs along outer edge of the nucleus. The axoneme possesses a  $9 \times 2 + 3$  microtubular pattern. Scale bar = 0.5  $\mu$ m. 4. Longitudinal section of spermatids. Note the aberrant organization: Axonemal basis (dC) located in front of implantation fossa near acrosomal vacuole; implantation fossa with granular dense material; nucleus strongly elongated, its anterior part triangular. Scale bar = 1  $\mu$ m. Abbreviations: AV = acrosomal vacuole, Ax = axoneme, dC = distal centriole, Fl = flagellum, IF = implantation fossa, M = mitochondria, Mm = manchette of microtubules, N = nucleus, NC = nuclear canal, Sp = spermatozoa, V = vesicles.





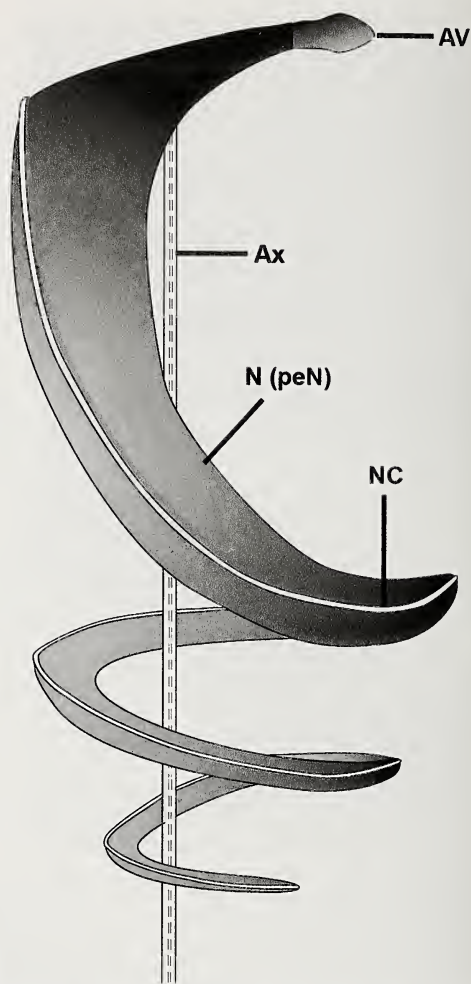


mium tetroxide. After washing, the specimens were rinsed in graded ethanol solutions (60%, 70%, 80%, 96%, absolute) and embedded in Spurr's resin (Spurr 1969). Ultrathin sections were made with a Leica ultramicrotome and stained with uranyl acetate and lead citrate (Reynolds 1963). Examination was performed with a Zeiss EM 10A electron microscope. For depository of voucher specimens see Knoflach & van Harten (2001).

Differentiation of the spermatozoa takes place in cysts which are surrounded by extensions of the somatic cells. These are located in the periphery of the relatively small testes. The spermatids are loosely distributed within these cysts (Fig. 1). In the following account, the shape of the main cell components of late-stage spermatids will be described, because this stage is most useful for comparative spermatological studies. A reconstruction of a late-stage spermatid is given in Fig. 5.

**Nucleus.**—In late-stage spermatids the nucleus is the most prominent component. It is strongly elongated and turns several times around the axoneme (Fig. 2). In cross-sections the main part of the nucleus forms a flattened ribbon (Figs. 2, 3). Only the anterior part is more or less lens-shaped, containing the axonemal basis and the implantation fossa (Fig. 4). Until the coiling process, the nucleus is surrounded by a manchette of microtubules (Fig. 3). In longitudinal sections the anterior part of the nucleus forms a triangle with the main part (postcentriolar elongation, see below) (Fig. 4). Along the outer edge of the nucleus runs a nuclear canal, which contains the acrosomal filament in its anterior part (Figs. 2, 3, 9).

**Implantation fossa and axoneme.**—During spermatogenesis normally an indentation of the nucleus is formed in front of the axonemal basis, the so-called implantation fossa. In *T. argo* the axonemal basis migrates to the anterior part of the nucleus and is finally located close to the acrosomal vacuole (Fig. 4). The implantation fossa extends behind the axonemal basis deeply into the postcentriolar elongation of the nucleus, which in *T. argo* constitutes the main part of the nucleus (Figs. 4, 5). Within the implantation fossa several globules and granules are accumulated which are very dense in mature spermatozoa (Figs. 6, 7). Embedded in this material, the proximal centriole is located extraordinarily far away



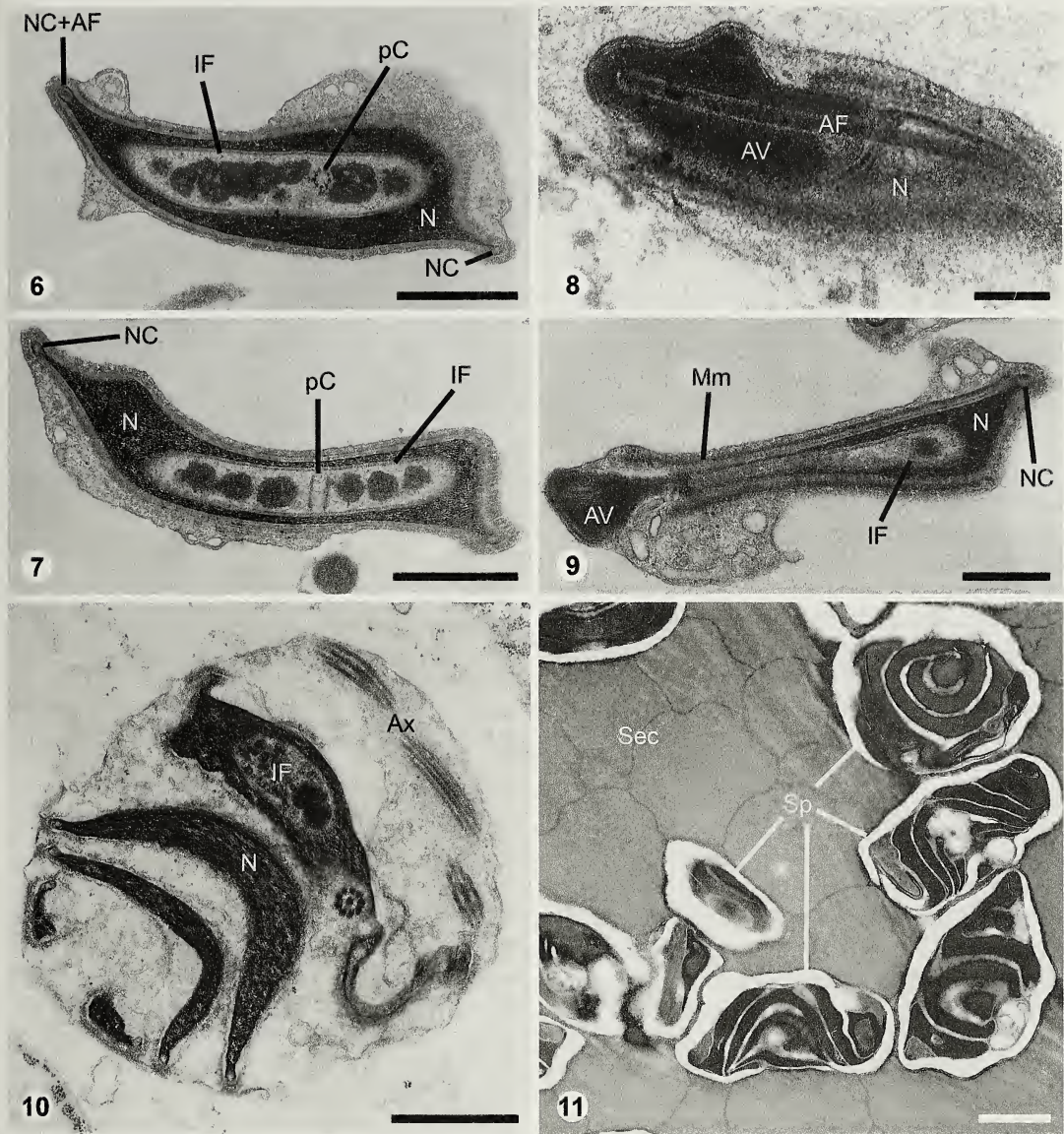
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Figure 5.—Schematic reconstruction of a late-stage spermatid of *Tidarren argo* (only main cell components shown). Note the elongated nucleus coiling several times around the axoneme. As a consequence of the extremely positioned axonemal basis close to the acrosomal vacuole the main part of the nucleus (behind the axonemal basis) can be determined as postcentriolar elongation of the nucleus (peN). Abbreviations: AV = acrosomal vacuole, Ax = axoneme, N (peN) = nucleus (postcentriolar elongation of the nucleus), NC = nuclear canal.

from the distal one (Figs. 6, 7). A reconstruction of a longitudinal section of the anterior part of a late-stage spermatid is given in Fig. 12. The axoneme possesses the  $9 \times 2 + 3$  pattern of microtubules (Fig. 3).

**Acrosomal complex.**—The acrosomal vacuole has an irregular arrowhead-shape (Fig. 8). The basis of the acrosomal vacuole is very





Figures 6–11.—Late-stage spermatids and mature spermatozoa of *Tidarren argo*. 6, 7. Sections of spermatids in the region of the implantation fossa. Note the proximal centriole located deeply within the implantation fossa which is filled with globular and granular dense material. Scale bars = 1  $\mu\text{m}$ . 8. Longitudinal section of the irregularly shaped acrosomal vacuole. Acrosomal filament starts at anterior part of acrosomal vacuole and continues into nuclear canal. Scale bar = 0.25  $\mu\text{m}$ . 9. Front part of spermatid. Note irregular shape of acrosomal vacuole. Manchette of microtubules around nucleus continues to acrosomal vacuole. The acrosomal filament seems very short, because of the empty nuclear canal close to the acrosomal vacuole. Scale bar = 0.5  $\mu\text{m}$ . 10. At the end of spermatogenesis the main cell components (nucleus, axoneme and acrosomal vacuole) coil within the cell. Scale bar = 1  $\mu\text{m}$ . 11. Section of spermatophore of palpal organ. Mature spermatozoa possess a thin secretion sheath and are embedded in a dense conspicuous secretion. Scale bar = 1  $\mu\text{m}$ . Abbreviations: AF = acrosomal filament, AV = acrosomal vacuole, Ax = axoneme, pC = proximal centriole, IF = implantation fossa, Mm = manchette of microtubules, N = nucleus, NC = nuclear canal, Sec = secretion, Sp = spermatozoa.

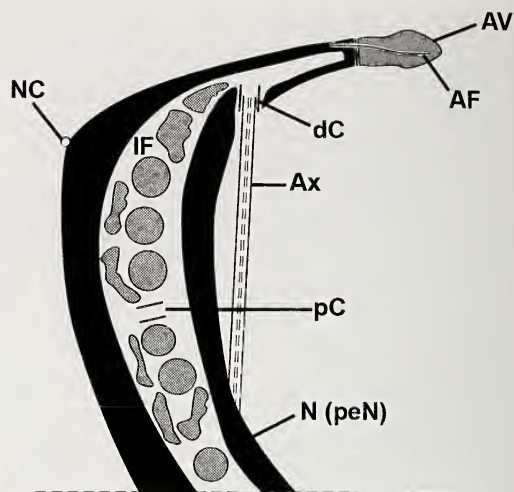


thin. A layer of dense material is located between the acrosomal vacuole and the nucleus (Fig. 9). The manchette of microtubules surrounds more than half of the acrosomal vacuole (Fig. 9). The subacrosomal space is narrow and contains the acrosomal filament which continues into the nuclear canal (Fig. 8, 9). The short acrosomal filament ends near the axonemal basis (Fig. 9).

**Additional cell components.**—Other cell components, e.g., mitochondria, Golgi apparatus, and vesicles are mainly seen in the cytoplasm of the posterior part of the spermatid. They seem to be absent in mature spermatozoa.

**Mature spermatozoa.**—At the end of spermatogenesis the spermatids coil. The main cell components (acrosomal vacuole, nucleus and axoneme) are involved in this coiling process within the sperm cell. The nucleus coils up to four times and the axoneme coils at the periphery of the cell (Fig. 10). Finally, in mature spermatozoa, which receive a secretion sheath, cell components are compact and tightly together (Fig. 11). The secretion sheath is rather thin and the mature spermatozoa are embedded in a conspicuous, dense secretion which apparently hinders the fixation process during preparation as seen in Fig. 11. A reconstruction of a section of a mature spermatozoon is given in Fig. 13. Interestingly, the mature spermatozoa are not densely packed in the spermophore of the palpal organ (Fig. 11).

The spermatozoa of *Tidarren argo* possess a highly derivative organization with most aberrant features in comparison to other spider species (e.g., Ōsaki 1969, 1972; Reger 1970; Boissin 1973; Alberti & Weinmann 1985; Alberti et al. 1986; Alberti 1990; Alberti & Coyle 1991; Michalik et al. 2003). Unfortunately, no other investigations dealing with fine structure of theridiid spermatozoa exist to allow an evaluation of our results. Hence, we compare the results mainly with our personal observations on other theridiid spiders (PM pers. obs.). On this evidence it appears that the spermatozoa of *T. argo* must be regarded as highly specialized, both within Theridiidae and within spiders in general. The nucleus of the *T. argo* spermatozoa is strongly elongated and ribbon-shaped over most of its length. As a consequence of the unusual position of the axonemal basis close to the acrosomal vacuole, the main part of the nucleus is represented



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Figure 12.—Schematic reconstruction of a longitudinal section of the front part of a late-stage spermatid in *Tidarren argo*. Note the proximal centriole which is embedded in the globular and granular dense material within the implantation fossa. The acrosomal filament extends only into the most anterior part of the nuclear canal. Abbreviations: AF = acrosomal filament, AV = acrosomal vacuole, Ax = axoneme, IF = implantation fossa, dC = distal centriole, pC = proximal centriole, N (peN) = nucleus (postcentriolar elongation of nucleus), NC = nuclear canal.

by the so-called postcentriolar elongation of the nucleus. In contrast, in our observations on *Argyrodes argyrodes* (Walckenaer 1842), *Crustulina guttata* (Wider 1834), *Nesticodes rufipes* (Lucas 1846), *Steatoda grossa* (C.L. Koch 1838) and *Theridion nigrovariegatum* Simon 1873, the nucleus is completely different, oval in cross section and more compact. The most striking features are the position of the axonemal basis and the extension and location of the implantation fossa. In *T. argo* the axonemal basis is located close behind the acrosomal vacuole in front of the implantation fossa. This arrangement completely differs from the above mentioned species. In the latter, the axonemal basis is located behind the implantation fossa which does not extend to the acrosomal vacuole, a situation typical for many other spider species (e.g., Alberti 1990; Alberti & Coyle 1991; Michalik et al. in press). The only exceptions in this respect known until now occur in the genera *Tetragnatha* and *Cyclosa* in which the implantation fossa also reaches the most anterior part of the



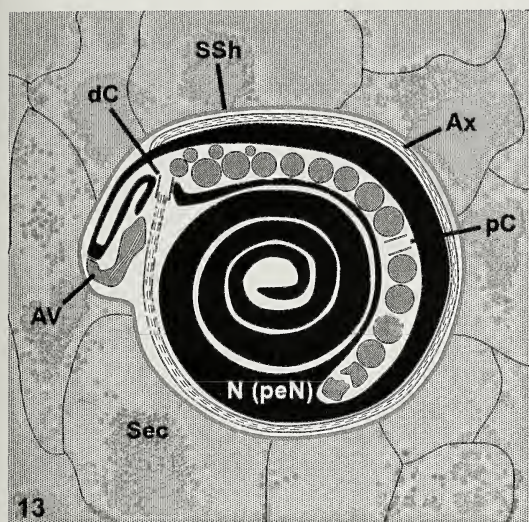


Figure 13.—Schematic reconstruction of a section of a mature spermatozoon in *Tidarren argo*. The nucleus coils as a spiral within the cell. The spermatozoon is surrounded by a thin secretion sheath and a considerable amount of dense secretion. Abbreviations: AV = acrosomal vacuole, Ax = axoneme, dC distal centriole, N (peN) = nucleus (postcentriolar elongation of nucleus), Sec = secretion, SSh = secretion sheath.

nucleus. However, in contrast to *T. argo*, in these species the axonemal basis is located in the posterior part of the implantation fossa as usual (Alberti 1990; Michalik et al. in press). Interestingly, in the theridiid spider *Neottiura bimaculata* (Linnaeus 1767) the position of the axonemal basis is similar to that seen in *T. argo*, but the nucleus and acrosomal vacuole are more compact, their shape therefore resembling that of other theridiid spiders. In *T. argo* the acrosomal vacuole shows an irregular arrowhead-shape and differs from the cylindrical or tube-like acrosomal vacuoles found in other theridiid species, e.g., *Argyrodus argyrodus* and *Theridion nigrovariegatum*. Of special interest is the dense secretion in which mature spermatozoa are embedded. Remarkably, the spermatozoa are loosely arranged in the palpal organ in comparison to other spider species, e.g., *Pachygnatha listeri* Sundevall 1830 (Michalik et al. in press). In this species no secretion was found and the spermatozoa have a thick protective secretion sheath. We suggest that in *T. argo* the protective function of the thick secretion sheath might be replaced by the copious secretion.

Interestingly, the secretions in which the spermatozoa are embedded clearly differ between different species. In each of the theridiid spiders observed above we found a different structural aspect of the secretion. Since other spider families show different types of secretions (unpublished observations by the authors), a great diversity in this feature is revealed. This may reflect specific importance in the process of reproduction. As nothing is known about the function of male secretions and their possible role in the female genital system, this is an interesting topic for future research.

*Tidarren argo* possesses highly derivative and aberrant spermatozoa in contrast to other theridiid species, but more investigations on further theridiid species are needed to develop evolutionary scenarios and to clarify a possible phylogenetic and functional relevance of spermatological characters. Furthermore, it would be important to know more about the function and chemistry of the secretion in which the mature spermatozoa are embedded.

#### ACKNOWLEDGMENTS

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## ON THE OCCURRENCE OF THE 9 + 0 AXONEMAL PATTERN IN THE SPERMATOOZOA OF SHEETWEB SPIDERS (ARANEAE, LINYPHIIDAE)

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**ABSTRACT.** In general, flagella and cilia of eukaryotes show an axoneme composed of a 9 + 2 microtubular pattern. However, the axoneme of spider spermatozoa is characterized by an exceptional 9 + 3 microtubular pattern, which is known as a synapomorphy of the Megoperculata (Amblypygi, Uropygi and Araneae). In contrast to all other observed spiders, the axoneme of the linyphiid spider *Linyphia triangularis*, was shown to lack the central microtubules thus representing a 9 + 0 axoneme. In the present study, we investigated the spermatozoa from several linyphiid species of different genera in order to show whether this peculiar pattern also occurs in other linyphiid spiders. Interestingly, in all observed species (*Neriene clathrata*, *N. peltata*, *Linyphia hortensis*, *Lepthyphantes* sp., *Oedothorax gibbosus*, *Gongylidium rufipes* and *Drapetisca socialis*) we found the 9 + 0 microtubular pattern in the axoneme. Since this study, although considering still a very limited number of species, includes species from Linyphiinae (Linyphiini and Micronetini) and Erigoninae it seems likely that this pattern is an autapomorphy of Linyphiidae.

**Keywords:** Sperm, phylogeny, axoneme, microtubules

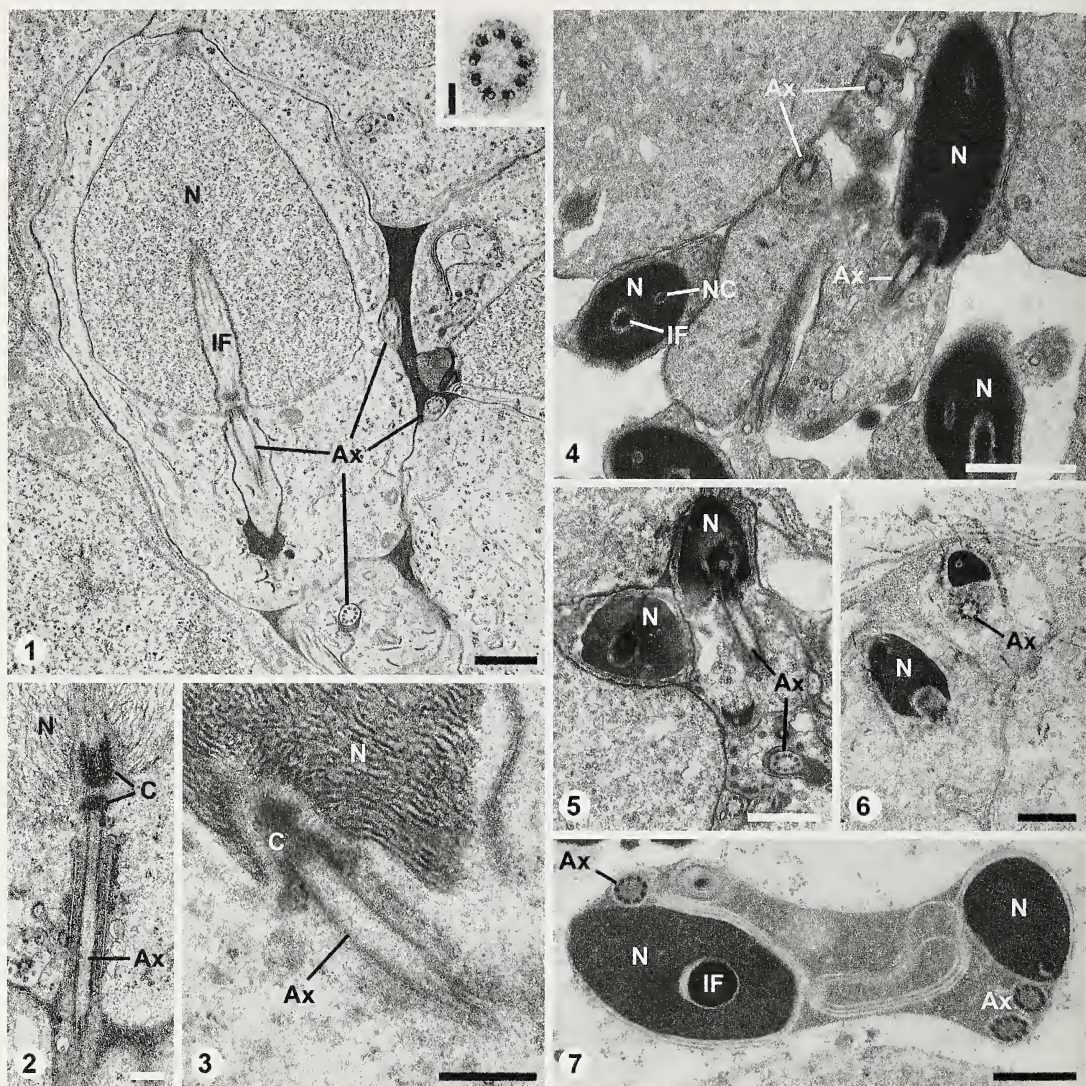
The typical and plesiomorphic axoneme found in eukaryote flagella and cilia possess a 9 + 2 arrangement of the microtubules. Nevertheless, there is a wide range of modifications within the axoneme of sperm flagella, e.g., in insects (Jamieson et al. 1999). Also within the Chelicerata a broader range of patterns occurs as shown by the recent species of the early derivative group, Xiphosura, where two different patterns are reported (9 + 2 and 9 + 0; Fahrenbach 1973; Yamamichi & Sekiguchi 1982; Alberti & Janssen 1986). Within arachnids only the spermatozoa of Scorpiones, Uropygi, Amblypygi, Araneae, Pseudoscorpiones and Ricinulei possess a flagellum (summary in Alberti 2000), in contrast to the spermatozoa of Solifugae, Acari, Palpigradi and Opiliones, which are aflagellate (the only exception is the opilionid genus *Siro* which shows an axoneme during the spermatogenesis; Juberthie et al. 1976; Alberti in press). The typical 9 + 2 pattern occurs only in Scorpiones, Pseudoscorpiones and Ricinulei. However, in Scorpiones aberrant patterns, e.g., 9 + 0 and 9 + 1 have also been reported (Hood et al. 1972; Jespersen & Hartwick 1973; Alberti 1983). The Uropygi, Amblypygi and Ar-

aneae (Megoperculata) possess as a synapomorphy a 9 + 3 pattern (summary in Alberti 2000; Michalik et al. 2003, 2004, in press and further personal observations). Thus it seems remarkable, that the linyphiid spider *Linyphia triangularis* (Clerck, 1757) has an unusual 9 + 0 axonemal pattern (Alberti 1990); unfortunately until now there have been no other ultrastructural observations on Linyphiidae spermatozoa to know assess if this pattern is typical of this taxon.

In the present study, we investigated the spermatozoa of several different linyphiid spiders from the subfamilies Linyphiinae (Linyphiini and Micronetini) and Erigoninae to begin a determination of the generality of this peculiar axonemal pattern within the Linyphiidae.

Male specimens of *Neriene clathrata* (Sundevall 1830), *N. peltata* (Wider 1834), *Linyphia hortensis* Sundevall 1830 (Linyphiinae, Linyphiini); *Lepthyphantes* sp. (Linyphiinae, Micronetini); *Oedothorax gibbosus* (Blackwall 1841) and *Gongylidium rufipes* (Linnaeus 1758) (Erigoninae); and *Drapetisca socialis* (Sundevall 1833) were dissected and fixed in 2.5% glutaraldehyde in 0.1 M phosphate buff-





Figures 1–7.—Spermatozoa of the observed linyphiid species. 1. Early spermatids of *Oedothorax gibbosus* with axonemes in cross—and longitudinal sections. Scale bar = 1  $\mu\text{m}$ . Inset: Detail of the axoneme of *Linyphia hortensis* in cross-section showing the 9 + 0 pattern. Scale bar = 0.1  $\mu\text{m}$ . 2–3. Posterior part of an early spermatid in longitudinal section. 2. *Neriene clathrata*. Scale bar = 0.25  $\mu\text{m}$ . 3. *Lepthyphantes* sp. Scale bar = 0.5  $\mu\text{m}$ . 4–6. Late spermatids. 4. *Drapetisca socialis*. Scale bar = 1  $\mu\text{m}$ . 5. *Gongylidium rufipes*. Scale bar = 0.5  $\mu\text{m}$ . 6. *Neriene peltata*. Scale bar = 0.5  $\mu\text{m}$ . 7. Coiled spermatid of *Linyphia hortensis*. Scale bar = 0.5  $\mu\text{m}$ . Abbreviations: Ax = axoneme, C = centriole, IF = implantation fossa, N = nucleus, NC = nuclear canal (canal containing the acrosomal filament).

er followed by postfixation in buffered 2% osmium tetroxide. After rinsing, the specimens were dehydrated in graded ethanols and embedded in Araldite or Spurr's resin (Spurr 1969). Ultrathin sections were made on a Leica ultramicrotome and the sections were stained with uranyl acetate and lead citrate (Reynolds 1963). The examination was performed with a Zeiss EM 10A electron micro-

scope. Voucher specimens have been deposited in the Zoological Museum of the University of Greifswald.

Spermiogenesis starts with spermatids which are mainly characterized by a large, roundish nucleus lying in a homogenous cytoplasm (Fig. 1). The axoneme migrates into the posterior pole of the nucleus (Figs. 1–4). The centrioles are orientated in the tandem po-



sition (Fig. 2). In all sections, the absence of the central tubules in the axoneme is obvious in all investigated species (Figs. 1–7) and in cross sections, the 9 + 0 axonemal pattern is evident (Figs. 1 inset, 4–7). Parallel to the migration of the axoneme, a deep posterior indentation into the nucleus is formed, the so-called implantation fossa (Fig. 1) which is filled with dense material at the end of spermatogenesis (Figs. 4, 7). At the end of spermatogenesis the nucleus coils once and the axoneme turns around the nucleus in the periphery of the cell (Fig. 7).

The occurrence of the 9 + 0 axonemal pattern is unique among the spermatozoa of Megopericulata and was first shown by Alberti (1990) for *Linyphia triangularis*. In spiders a 9 + 3 pattern normally occurs and was studied in detail by Dallai et al. (1995). The present study shows the peculiar 9 + 0 pattern for all observed Linyphiidae. Based on these observations many questions arise concerning the function and the phylogenetic impact of this character. Unfortunately, no studies on the movement of linyphiid spermatozoa exist. However, it was shown from other animal species that an axoneme which lacks the central tubules can still move. For example, Ishijima et al. (1988) compared the beat pattern from Asian and American horseshoe crabs. The Asian species *Tachypleus gigas* (Müller 1785) possess a 9 + 0 axoneme which beats in helical waves, in contrast to the planar waves of the 9 + 2 axoneme of the American horseshoe crab *Limulus polyphemus* (Linnaeus 1758). Similar results were also reported in the detailed studies of Gibbons et al. (1983, 1985) on the eel *Anguilla anguilla* (Linnaeus 1758) which possess spermatozoa with a 9 + 0 axoneme which lacks the central tubules as well as other structures, e.g., outer dynein arms, radial spokes and spokeheads. The spermatozoa of the eel beats in helicoidal waves. Hence it can be assumed that the spermatozoa of Linyphiidae are motile and the movements of the axoneme are different from those of other spider spermatozoa that possess a 9 + 3 axoneme. More investigations are needed to test this hypothesis and clarify the possible influence (selective advantage?) within the female genital system.

Furthermore, the occurrence of the 9 + 0 axonemal pattern in all observed species of linyphiids supports the assumption of Alberti

(1990) that this peculiar pattern might be an autapomorphy of Linyphiidae. Therefore it would be of much interest to know the situation in the supposed sister taxon Pimoidae as well as in the other linyphiid subfamilies (e.g., Hormiga 1994a, b; 2000).

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## EVIDENCE FOR DIRECTIONAL SELECTION ON MALE ABDOMEN SIZE IN *MECOLAESTHUS LONGISSIMUS* SIMON (ARANEAE, PHOLCIDAE)

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**ABSTRACT.** Abdomens of male *Mecolaesthus longissimus* Simon 1893 are on average more than twice as long as in females, their length is highly variable, and they show extremely steep allometric values when scaled on body size (OLS,  $b = 2.64$ ). Males cohabit with females, and they likely fight to defend this position as other pholcid spiders do. Male legs, which are usually used in pholcid male-male fights, do not show the usual high allometric values but a very low value (OLS,  $b = 0.37$ ). Collectively, this lends support to the idea that *M. longissimus* males do not use their legs in fights and that male abdomens have assumed a role in male-male fights. However, behavioral data are missing and sexual selection by female choice or inter-male display might be involved. A large sample of data from taxonomic revisions is used to document that across pholcids, males consistently have longer tibiae I (and probably legs in general) than females. Several possible reasons have been suggested to account for longer male than female legs in various spider groups, but the pattern in pholcids remains to be explained.

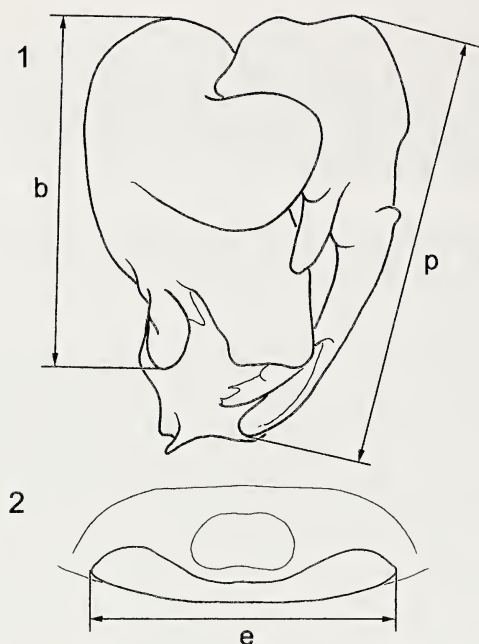
**Keywords:** Sexual size dimorphism, sexual selection, allometry, Pholcidae

Extreme sexual size dimorphism in spiders has attracted considerable attention for a long time and its evolutionary origin has fueled a lively and ongoing debate (Vollrath & Parker 1992; Coddington et al. 1997; Head 1995; Prenter et al. 1997, 1998, 1999; Hormiga et al. 2000; Schneider et al. 2000; Moya-Laraño et al. 2002; Walker & Rypstra 2003). The more common case of slight size dimorphism and the rather exceptional case of males being larger than females have remained comparatively out of the main focus of size dimorphism studies in spiders (but see Prenter et al. 1995, 2003; Toft 1989; Schütz & Taborsky 2003). Different selective forces, both natural and sexual, probably interact in many species, but fecundity selection may be the single major factor responsible for females usually being larger than males (Beck & Connor 1992; Elgar 1992; Head 1995; Prenter et al. 1999). However, simple size measures derived from the taxonomic literature may result in an overly simplistic view of dimorphism. Depending on the structure measured, either males or females may appear to be the 'larger' sex, and some or most dimorphism may be in shape rather than in size (Prenter et al. 1995).

Few cases of males being larger than females are known in spiders (Prenter et al.

1999; Lång 2001) even though large male size advantage has been documented in numerous species (Vollrath 1980; Elgar & Nash 1988; Nielsen & Toft 1990; Dodson & Beck 1993; Kotiaho et al. 1997, 1999; Elgar 1998; Elgar & Fahey 1996; Taylor et al. 2001; Prenter et al. 2003; Schaefer & Uhl 2003). In most cases in which males are larger than females, male-male fights are intense, and winners of contests sire a significant proportion of their mate's offspring (Rovner 1968; Watson 1990; Elgar 1998). Selection is particularly strong on the fighting structures per se (e.g., chelicerae in certain linyphiid and salticid spiders: Rovner 1968; Toft 1989; Pollard 1994; Funke & Huber In press) and such intense directional selection usually results in high allometric values (i.e.  $> 1.0$ ; Petrie 1992; Green 1992; Baker & Wilkinson 2001; Tatsuta et al. 2001; Funke & Huber In press; see also Eberhard et al. 1998; Eberhard 2002a, b). Natural selection may also result in males being the larger sex, as in the exceptional case of the water spider, *Argyroneta aquatica* (Clerck 1757). In this species, males are on average nearly 30% larger than females, as a result of the unusual habitat (Schütz & Taborsky 2003).

The presence and degree of sexual size dimorphism within and among species can be



Figures 1, 2.—*Mecolaesthus longissimus*, genital characters measured. 1. Bulb length (b) and procursus length (p), dorsal view; 2. Epigynum width (e), ventral view.

used to generate behavioral hypotheses that can then be tested. In this study, I have two main objectives: (1) to document and quantify the apparently unique dimorphism observed in the pholcid *Mecolaesthus longissimus*, and (2) to use data from the literature to quantify leg length dimorphism across pholcid species.

The main object of this study, *Mecolaesthus longissimus* Simon 1893, is endemic to the Cordillera de la Costa in northern Venezuela (Huber 2000). Nothing is known about its biology except for some very basic habitat data (Simon 1893; Huber 2000).

## METHODS

Males and females of *Mecolaesthus longissimus* were collected in a forest above Colonia Tovar (10°25'N, 67°18'W), 2100 m a.s.l., Aragua, Venezuela, on 26 November 2002, by the author. The present analysis is based on a sample of 30 males and 14 females preserved in 80% ethanol. They are presently deposited at the Zoological Research Institute and Museum Alexander Koenig, Bonn, but will later be partly transferred to the Museo de La Salle, Caracas. Drawings were made with a camera lucida on a Leitz Dialux 20 compound micro-

scope. Photos were made with a Nikon Coolpix 995 digital camera (1600 × 1200 pixels) mounted on a Nikon SMZ1500 dissecting microscope.

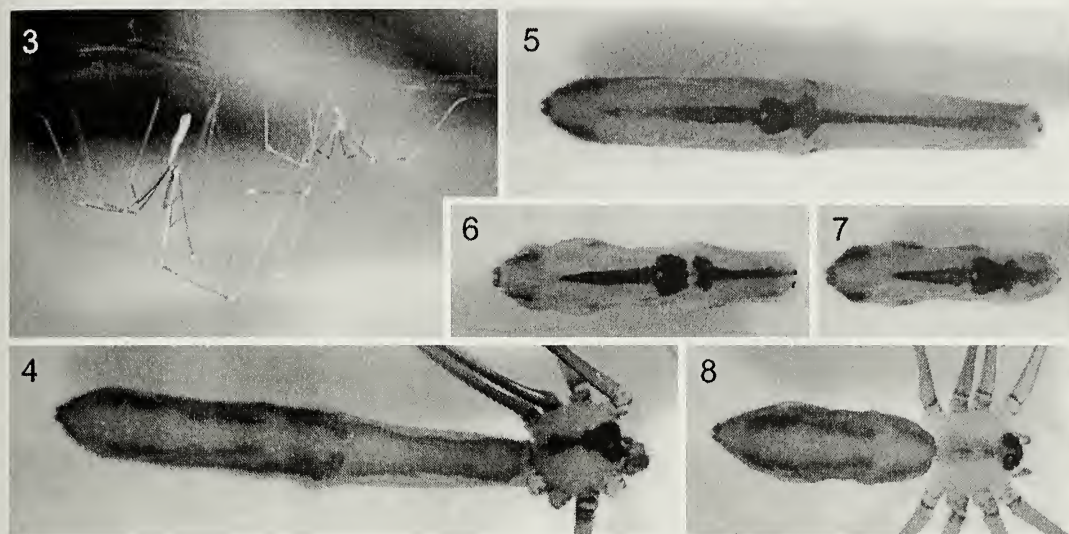
Measurements were made with an ocular grid on a Nikon SMZ1500 dissecting microscope. Tibia length was measured dorsally; carapace length was measured medially from anterior median eyes to posterior border; abdomen length was measured ventrally from frontal end to base of frontal spinnerets; anterior and posterior parts were divided by the epigastric furrow, resulting in two measures; for genitalic measures see Figs. 1 and 2. Genitalia were included in the analysis to support the assumption that all specimens included are indeed the same species. Statistical analysis was done with SPSS 11.0. Ordinary least squares (OLS) and reduced major axis (RMA) regressions of log-transformed characters were calculated for all traits on carapace length as an indicator of body size (for critique and justification of method see Green 1999 and Eberhard et al. 1999). Carapace length was used rather than carapace width (the usual indicator of body size in spiders) because lateral carapace borders appeared too soft and indistinct.

For comparison of male and female tibia 1 lengths in pholcid spiders, data were taken from recent revisions (Huber 1997a, b, c, 1998a, b, 2000, 2001, 2003a, b, c; Huber & Pérez 1998, 2001; Huber et al. In press; B.A. Huber unpubl. data). In order to be included in the analysis, the species (re)description had to give a mean value of at least five measured tibiae 1 in each sex. All together, 2673 tibia 1 measures of 100 species (20 of them unpublished) were included, representing 28 genera and all four pholcid subfamily-level taxa. The complete data matrix is available from the author.

## RESULTS

**Morphometric analysis of *Mecolaesthus longissimus*.**—Three details are noteworthy in the morphometric analysis (Table 1). First, male abdomens are on average more than twice as long as female abdomens (see also Figs. 4, 8, 9). Second, male abdomens are extremely variable (see also Figs. 5–7 & 9). Third, it is the anterior part of the male abdomen that accounts for most of the variation in male abdomen length. In females, to the





Figures 3–8.—*Mecolaesthus longissimus*. 3. Male (left) and female in the web (photo courtesy B. Striffler); 4. Large male, dorsal view; 5–7. Large, medium, and small male abdomens, ventral views; 8. Medium size female. Figs. 4–8 are to the same scale.

contrary, it is the posterior part of the abdomen that is much more variable than the anterior part.

No appreciable shape variation was seen in the structures usually used in species discrimination in pholcids (male procurus, bulbal sclerites, cheliceral armature). The regression coefficients of the three genitalic structures measured were low as is usual for genitalia (Eberhard et al. 1998). Surprisingly low regression values were also found for male (but not female) legs.

#### Comparative analysis of pholcid tibiae

**1.**—There is a consistent trend for males to have longer tibiae 1 than females when 100 species were compared (Fig. 10). The mean ratio of male/ female tibia 1 is 1.28, the median 1.27 (Fig. 11). Strictly speaking, species are linked by phylogeny and not independent data points (Harvey & Pagel 1991). However, my aim here is to document a universal trend within the family and not to claim that there are independent events that might justify some adaptive explanation. Regardless of the details of the phylogeny of pholcids, parsimony clearly suggests that ancestral pholcids had longer male than female legs.

#### DISCUSSION

The extremely high allometric value of male abdomen length in *M. longissimus* indicates that directional selection is operating

on this body part. Structures used as weapons in male-male fights or as visual display characters in the context of sexual selection tend to show high allometric values (Petrie 1992; Green 1992; Baker & Wilkinson 2001; Tatsuta et al. 2001; Funke & Huber In press; see also Eberhard et al. 1998; Eberhard 2002a, b). The exact nature of this selection cannot be derived from allometric values alone but only by behavioral observations and experiments. However, circumstantial evidence suggests that males might use their abdomens in a most unusual and unexpected way: as display or even fighting devices.

First, male-female postinsemination non-contact guarding (*sensu* Alcock 1994) is rare in spiders (Elgar 1998) but common in pholcids (Eberhard & Briceño 1985; Kaster & Jakob 1997; pers. obs.). For example, during a monthly survey of a population of *Modisimus guatuso* Huber 1998 in Costa Rica from November 1995–September 1997, I counted 398 pairs involving adult males and adult females, not a single pair involving a juvenile female, and 65% of 596 males seen were cohabiting (unpub. data). During several collecting expeditions I have become used to the expectation that seeing one adult pholcid often means that another one of the opposite sex is nearby. Most webs at the collection site of the present species contained a male and a mature female.

Table 1.—*Mecolaesthus longissimus*, male and female characters measured (in mm), with sample sizes (*n*), ranges, means, standard deviations (SD), coefficients of variation, corrected for sample size (CV\*), significance values of Kolmogorov-Smirnov tests for normal distribution (KS), estimates on measurement error ( $\pm 1/2$  unit on the measuring grid), and slopes (b) of regressions on carapace length as an indicator of body size, using ordinary least squares (OLS) and reduced major axis (RMA) regression. Slopes significantly different from 0 are indicated by \*(*P* < 0.05), \*\*(*P* < 0.01), and \*\*\*(*P* < 0.001). RMA regressions were not calculated when OLS values were non-significant.

Characters	<i>n</i>	Range	Mean	SD	CV*	KS	Measure- ment error ( $\pm$ mm)	b (OLS)	b (RMA)
Males									
tibia 1 length	30	10.53–12.80	11.59	0.54	4.7	0.57	0.07	0.37***	0.57
tibia 3 length	30	5.15–6.40	5.78	0.31	5.3	0.69	0.05	0.49***	0.66
abdomen total length	30	2.90–6.50	4.85	1.21	25.1	0.33	0.07	2.64***	3.14
abdomen frontal part	30	1.15–3.80	2.42	0.90	37.5	0.32	0.03	3.72***	4.67
abdomen post. part	30	1.75–2.95	2.44	0.36	15.1	0.75	0.07	1.60***	1.93
carapace length	30	0.90–1.22	1.09	0.088	8.2	0.84	0.01	—	—
bulb length	30	0.35–0.38	0.36	0.009	2.4	0.10	0.005	0.21***	0.29
procursus length	30	0.39–0.43	0.41	0.012	2.9	0.16	0.005	0.23***	0.35
Females									
tibia 1 length	10	6.55–8.10	7.38	0.46	6.4	0.71	0.07	1.91**	2.37
tibia 3 length	14	3.05–3.78	3.51	0.21	6.1	0.71	0.03	1.39**	2.11
abdomen total length	14	2.00–2.70	2.34	0.18	7.9	1.00	0.02	1.07 n.s.	—
abdomen frontal part	14	0.82–0.92	0.88	0.031	3.6	0.52	0.02	0.45 n.s.	—
abdomen post. part	14	1.17–1.80	1.46	0.17	11.6	1.00	0.02	1.43 n.s.	—
carapace length	14	0.80–0.90	0.85	0.026	3.1	0.78	0.01	—	—
epigynum width	14	0.34–0.39	0.36	0.013	3.6	0.90	0.005	0.37 n.s.	—

(The reason that many more males were collected is simply that I always collected the males first in order to maximize the male sample, and females often dropped out of the web before I could capture them.) *Pholcus phalangioides* (Fuesslin 1775), the pholcid species

studied in most detail, is apparently unusual in this regard as there is no evidence for mate guarding (Uhl 1998).

Fights have been observed in pholcids (Eberhard 1992; Eberhard & Briceño 1985), and it is probable that males gain something by cohabiting with or guarding females and that they will fight to defend whatever resource there is. The exact benefit males derive from staying with females is unknown. They might protect their sperm investment from competition with rival male ejaculates, because in pholcids the second males may fertilize a large proportion of eggs (Eberhard et al. 1993; Kaster & Jakob 1997; Yoward 1998; Schäfer & Uhl 2002). They might improve female foraging efficiency, but chivalrous behavior in pholcids might rather be a means to induce the female not to leave and thus make her defensible (Eberhard & Briceño 1983). They might aid the female to repel other motivated males (Parker 1970). Finally, they might provide postinsemination signals to increase their chances of fathering their mate's

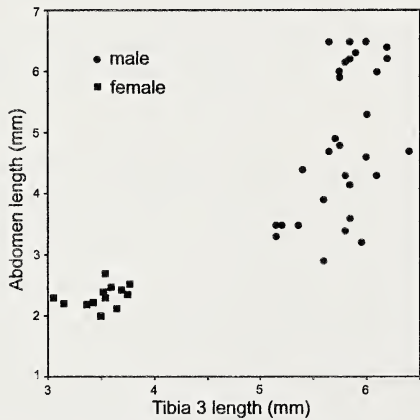
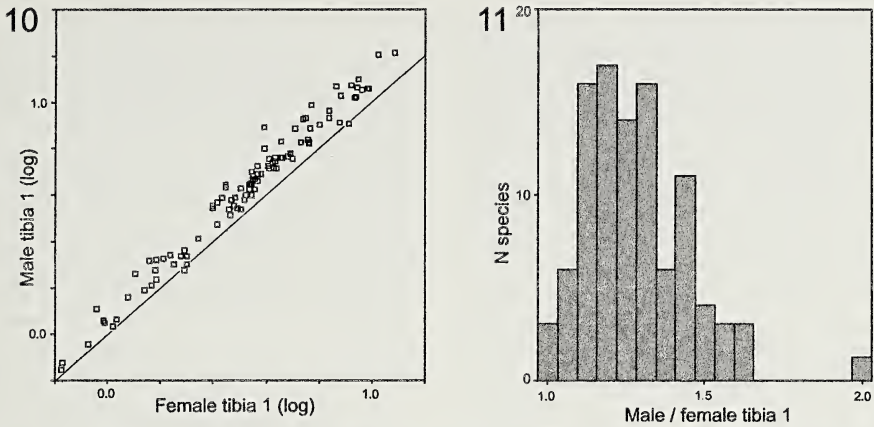


Figure 9.—*Mecolaesthus longissimus*, scatter of male and female abdomen lengths on tibia 3 lengths.





Figures 10, 11.—Tibia 1 length dimorphism in Pholcidae. 10. Scatter of log-transformed male tibia 1 lengths on female tibia 1 lengths for 100 pholcid species. The line indicates monomorphism; 11. Histogram showing the ratio of male/female tibia 1 lengths in 100 pholcid species.

offspring (Eberhard 1985; Alcock 1994). Whatever the details, male *M. longissimus* probably fight intruders, or try to expel residents.

Second, exaggerated morphologies and high variability of sexually dimorphic characters often seem to result from sexual selection (Pomiankowski & Møller 1995; Baker & Wilkinson 2001). For example, extreme male size variation in the salticid *Zygoballus rufipes* Peckham & Peckham 1885 was attributed to alternative male mating strategies (Faber 1994). Comparative evidence strongly suggests that female *M. longissimus* have retained the plesiomorphic abdomen size, and that males vary from ‘normal’ to extreme. All other known species of *Mecolaesthus* have ‘normal’ abdomens, not appreciably different from the abdomens of females and of other closely related genera (Huber 2000). Thus, male *M. longissimus* abdomens are exaggerated sexual modifications.

Third, there is no evidence pointing to ecological determinants of male abdomen size. The webs in which the specimens were collected appear identical to those of many New World pholcids, i.e. a distinct, loosely meshed and more or less domed sheet (Eberhard & Briceño 1985). Further observations on ecology are not available.

Thus, sexual selection on male abdomen size appears as the most plausible explanation for the dimorphism in this species. Female choice might be involved, and a large abdomen may be a costly and thus honest indicator

of male quality (cf. Uetz et al. 2002). Alternatively, cryptic female choice might select for exaggerated male testes or accessory genital glands (cf. Eberhard 1996). However, numerous studies indicate that male-male fights are the most important force selecting for large male size (Christenson & Goist 1979; Watson 1990, 1991; review in Andersson 1994). Therefore, I hypothesize that male *M. longissimus* use their abdomens either to fight or to assess each other before fights. A large brown spot ventrally on the abdomen (Figs. 5–7) might be significant in this respect: the spot marks the posterior border of the anterior part of the abdomen, i.e. that part that is most extremely size dimorphic, has the highest regression coefficient, and is therefore the most reliable predictor of male size (cf. Taylor et al. 2000). Male *M. longissimus* carry their abdomen more or less vertically (Fig. 3; see also fig. 439 in Simon 1893), making the spot potentially visible to conspecifics in the same web. Whether pholcids have the appropriate visual capabilities is unknown.

A surprising but revealing result is the low regression value of male (but not female) tibia 1 ( $b[OLS] = 0.37$ ) in *M. longissimus*. It is consistently higher in other pholcids studied: 0.88 in *Metagonia mariguitarensis* (González-Sponga 1998) (Huber 2004), 1.00 in *Buitinga safura* Huber 2003 (Huber & Hopf 2004), 1.22 in *Physocyclus globosus* (Taczanowski 1874) (Eberhard et al. 1998). This would seem to indicate stabilizing selection in *M. longissimus*, in contrast to other pholcids. I hypoth-

esize that the unusual regression value of male leg length and the unusual exaggerated abdomen are directly correlated and that *M. longissimus* males have changed from leg fights (the usual strategy in pholcids; Eberhard 1992; Eberhard & Briceño 1985) to abdomen fights, thus relaxing selection on leg length. However, this still requires an explanation for longer legs in *M. longissimus* males than in females. One potential explanation is phylogenetic inertia, as nearly all pholcids have longer male than female legs (see below).

The tibia I measures across the entire family clearly show that male pholcids have consistently longer tibiae than females. Unfortunately, there are no comparable data on other size measures, as for example total body size. However, the reason for this missing data is that male and female pholcids usually are monomorphic regarding total size (Elgar 1992; pers. obs.). Collectively, this lends further support to the idea that single size measures may not reliably reflect sexual size dimorphism in spiders (Prenter et al. 1995). The reasons for leg length dimorphism in pholcids are unknown. Longer legs may help cursorial males in their search for females (Montgomery 1910), they may provide males with a wide sensory radius and keep them relatively safe from female aggression (Elgar et al. 1990), or they may play a role in male-male fights (Eberhard 1992; Dodson & Beck 1993; Eberhard & Briceño 1985; Prenter et al. 1995; Bridge et al. 2000). Whatever the details, the consistent and fairly uniform pattern argues for a widely responsible cause or set of causes rather than for varying explanations in different taxa.

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## EFFECTS OF PREY QUALITY ON THE LIFE HISTORY OF A HARVESTMAN

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**ABSTRACT.** Information on the value of various food types for harvestmen is sparse. The aim of this study was, therefore, to clarify the quality of six different food types to a harvestman. Survival, growth and development were used as measures of fitness in a laboratory experiment. Recently hatched *Oligolophus tridens* were fed the following experimental diets until maturity: *Drosophila melanogaster* (Diptera), entomobryid Collembola (*Tomocerus bidentatus*/*Sinella curviseta*), *Folsomia candida* (Collembola), *Sitobion avenae* (Aphidoidea), *Rhopalosiphum padi* (Aphidoidea), and a mixed diet containing the five prey types. Survival and growth rate were high on the *D. melanogaster* and entomobryid diets, and low on the *F. candida*, *S. avenae* and *R. padi* diets. The mixed diet caused a high early mortality, later a good survival and a high growth rate. The majority of harvestmen on the *D. melanogaster* and entomobryid diets matured. None of the harvestmen fed pure aphid diets developed beyond the fourth instar, and only few from the *F. candida* diet matured. Overall, the diets separate in three levels: *D. melanogaster* and the entomobryid diet were high-quality, the mixed diet was intermediate, and the two aphid diets and *F. candida* diet were low-quality. In general, the quality ranking agrees with that of other generalist predators, though there are differences in details.

**Keywords:** Opiliones, *Oligolophus tridens*, fitness, diet

Harvestmen are omnivorous generalists, with a variety of feeding habits, ranging from plant eating to predation. They eat a range of small invertebrates, which are probably caught live and killed. Examples of the invertebrate diet are: springtails, aphids, snails, earthworms, other harvestmen and spiders (Sankey & Savory 1974). Harvestmen are also scavengers and will scavenge both on invertebrates (Sankey & Savory 1974) and vertebrates (Sankey 1949). Studies have shown that harvestmen generally prefer small prey, such as Hemiptera and Collembola (Adams 1984). In the laboratory, harvestmen have successfully been fed odd diets, e.g., bananas, cooked vegetables, ham, cream cheese (Gnaspi 1996), dried eggs, whole meal flour, yeast (Todd 1949), together with live animal food. Gnaspi (1996) tested which food types the harvestman *Goniosoma spelaeum* (Mello-Leitão 1932) will accept and came to the conclusion that these harvestmen should be considered “omnivores tending to carnivory”. There are only few laboratory studies of the feeding ecology of harvestmen, so information on the quality of specific diets is very sparse.

Laboratory studies on the quality of differ-

ent food types have been conducted on several generalist predators such as spiders (Toft 1995; Toft & Wise 1999a) and carabid beetles (Bilde & Toft 1999). The quality of different prey can be evaluated by comparing fitness parameters of the predator kept on different dietary treatments. Different fitness parameters can be used as quality measures: survival, body mass, time used in development, size of body parts, fecundity etc. In this study, survivorship, growth and development were used. Young harvestmen (*Oligolophus tridens* (C.L. Koch 1836)) were reared on six diets and the quality of each diet was assessed by comparison of the fitness measures. In the experiment we tested monotypic diets of a fly, two springtails, two aphids, and a mixed diet of all five. These prey types were chosen because they represent ordinary harvestman prey from different invertebrate orders and most of the prey can be found in the same habitats as *O. tridens*. Furthermore, the aphids (*Sitobion avenae* (Fabricius) and *Rhopalosiphum padi* (Linnaeus)) are pests in agricultural fields, and are among the most abundant aphids in cereal fields (Wikteli 1982).

The prey types used in the present study



have been evaluated in other studies of generalist predators as well. In the light of these results we expected that fruit flies, *Drosophila melanogaster* (Meigen), and the entomobryid springtails *Tomocerus bidentatus* (Folsom)/*Sinella curviseta* (Brook) would be of good quality to the harvestmen (Toft & Wise 1999a; Vanacker et al. 2004). The aphids *S. avenae* and *R. padi* and the collembolan *Folsomia candida* (Willem) are of poor quality to spiders and carabid beetles. Only a few individuals molted when wolf spiders (*Pardosa prativaga* (L. Koch 1870)) were fed the aphids (Toft 2000). Wolf spiders (*Schizocosa* sp.) fed *F. candida* survived for a shorter period than the starved controls (Toft & Wise 1999a) and *F. candida* was therefore considered a toxic prey. We expected that these findings would also apply to harvestmen, because both wolf spiders and harvestmen are generalist predators and can be found in the same habitats. It is more difficult to predict the consequences of the mixed diet. The effect depends on the effect of each prey type, how much the harvestmen eat of each prey and if there is an interaction of the effects between some of the prey when harvestmen are fed a mixed diet.

## METHODS

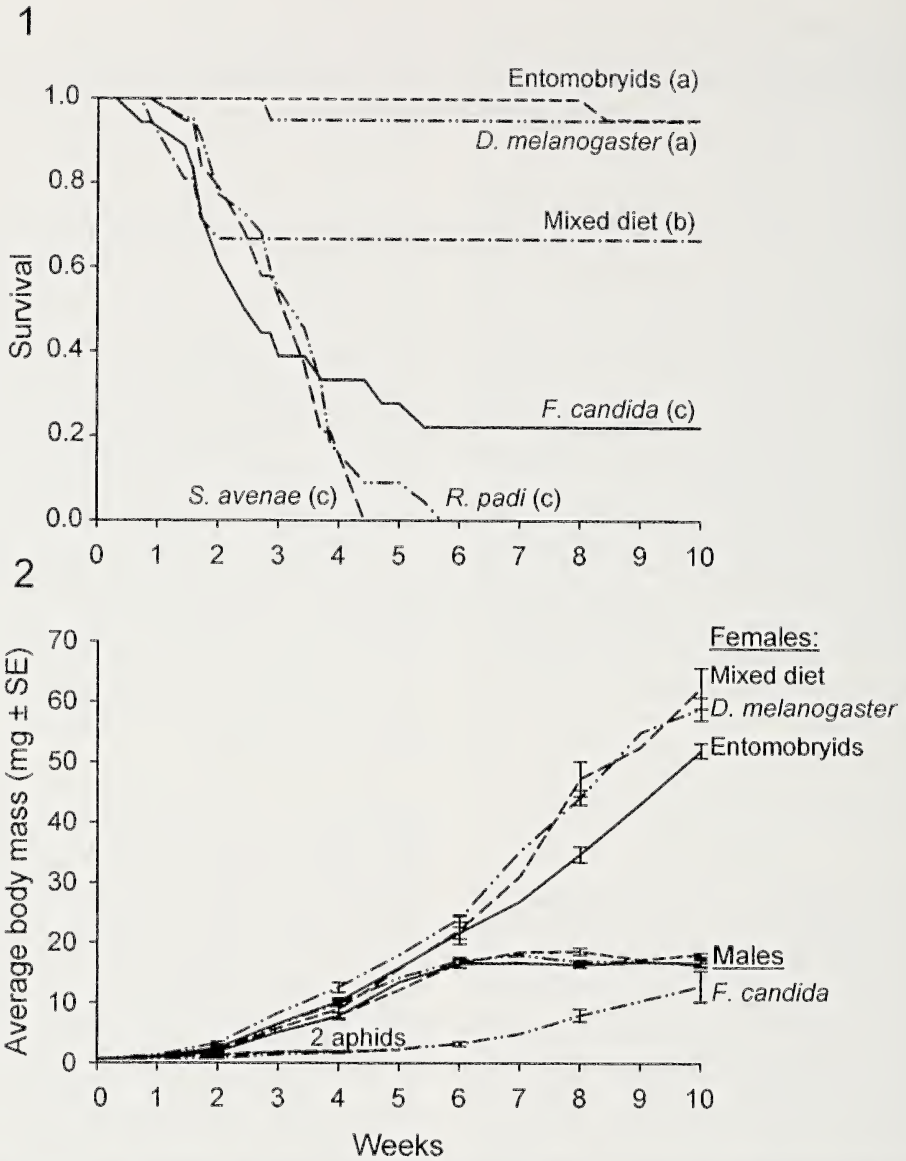
**The harvestman.**—The harvestman *Oligolophus tridens* occurs all over northern and central Europe (Martens 1978) and has also been reported from North America (Bell 1974). The species is abundant in Denmark and can be found in a variety of habitats, especially in woodlands, roadsides and in gardens. The harvestman has a body length of 4–5 mm (males) or 5–6.5 mm (females) (Sankey & Savory 1974). The life cycle is annual and the harvestmen overwinter in the egg stage. Hatchlings emerge in spring (in Denmark April–May, Meinertz 1964; per. obs.). The first molt takes place a few hours after the harvestmen emerge from the egg (Martens 1978) and they pass through 6 juvenile instars before they mature (Pfeifer 1956; Phillipson 1962).

**Prey.**—All the prey animals came from laboratory cultures. The prey was freeze killed and provided in surplus amounts. Wild type fruit flies (*Drosophila melanogaster*) were reared on instant *Drosophila* medium (Formula 4–24, Carolina Biological Supply; Burlington, NC, USA) mixed with crushed dog

food (Techni-Cal® ADULT, Martin Pet Foods, Ontario, Canada) in a proportion of 100 g of *Drosophila* medium to 54.5 g dog food. The enrichment ensured a high nutritional quality of the flies, especially regarding proteins. Enriched fruit flies increased growth and survival in a wolf spider (Mayntz & Toft 2001) and supported a high egg production in a carabid beetle (Bilde et al. 2000). *Folsomia candida* was raised on baker's yeast. The entomobryids *Tomocerus bidentatus*/*Sinella curviseta* were both raised on baker's yeast and *Drosophila* medium. At the beginning of the experiment the harvestmen in the entomobryid group were fed *T. bidentatus*, but as the culture was slow and there was a risk of food shortage, the harvestmen were fed *S. curviseta* from week 6. Both *T. bidentatus* and *S. curviseta* are considered to be prey of high quality (*T. bidentatus*: Toft & Wise 1999a; *S. curviseta*: Vanacker et al. 2004). *Rhopalosiphum padi* and *Sitobion avenae* were both raised on wheat seedlings of mixed cultivars. Mixed stages of springtails and aphids were used to feed the harvestmen.

**The experiment.**—Young *O. tridens* in the second instar were collected in a small forest near Århus, Denmark, 56°07'N, 10°00'E, in late April 2003 by sifting leaf litter over a white tray. The harvestmen were kept individually in plastic tubes (diameter 2 cm, height 6 cm) with a moistened bottom layer of plaster mixed with charcoal and a foam rubber plug. Throughout the experiment the harvestmen were kept at a constant temperature of 17 °C, and a photoperiod of 16L:8D. The harvestmen were weighed the day after collection and assigned to one of six diet treatments with roughly the same distribution of body masses. The treatments were: *D. melanogaster*, *T. bidentatus*/*S. curviseta* (both Entomobryidae), *F. candida* (Isotomidae), *S. avenae*, *R. padi*, and a mixed diet with about equal amounts of the five prey types. Some of the replicates were discarded because of escapes and accidents. The number of replicates in each treatment therefore varied from 18–22. The harvestmen were transferred to larger plastic tubes (diameter 3.5 cm, height 8 cm) after the third molt.

Prey and water were renewed, and mortality and molts were checked three times per week. The duration of instar 2 was recorded as the number of days from collection to the next



Figures 1-2.—1. Survivorship curves for harvestmen *Oligolophus tridens*. The harvestmen were raised in the laboratory from the second instar to maturity on six different diets. Curves with different letters are significantly different. 2. Growth curves for harvestmen *Oligolophus tridens*. The harvestmen were raised in the laboratory from the second instar to maturity on six different diets. “Males” are males from the diets: *Drosophila melanogaster*, entomobryid springtails and mixed diet. Harvestmen fed aphids died before the sex could be determined. *Folsomia candida* data for males and females were pooled because of the low number. Error bars are only shown every second week for the sake of clarity.

molt. A few molts were missed. As the molts progressed synchronously within each diet treatment a molt date was estimated for the missing molts, using the average molt date for the harvestmen in the same treatment. When a molt was observed, the midpoint between two days in which the tubes were checked,

was used to compute the parameter “days in instar”. The harvestmen were weighed weekly (Sartorius electronic balance MC5; 0.001 mg accuracy) to measure growth rate. The most recent weighing before the molt was used for the parameter “weight at molt”. The experiment was terminated after 10 weeks.



**Statistical analysis.**—The survivorship data were tested with the Log Rank test (Pyke & Thompson 1986). The pairwise Log Rank comparisons were not corrected with sequential Bonferroni adjustment (Moran 2003), because the prey types were chosen based on prior assumptions and the relatively high number of prey types would make it unreasonably difficult to obtain any significance after adjustment. The growth curves were compared using multivariate analysis of variance (MANOVA) with repeated measures, with time (weeks) as the repeated factor. The time \* diet interaction term was used to detect differences in growth over time between the treatments. However, animals that died before the end of the experiment were excluded from the analysis. We analyzed the growth data for all treatments for only three weeks or approximately 50% of their maturation time, at which time there were still harvestmen in all treatments. Body mass changes from start of the experiment to week three were tested with one-way ANOVA. The data were log transformed to achieve variance homogeneity (Levene's test  $\alpha > 0.05$ ). A post hoc test was used to locate the differences indicated in the overall ANOVA; because the treatments were chosen to test potential harvestman food, and all the comparisons therefore were planned, a Student's t-test was applied. For the treatments: *D. melanogaster*, entomobryids and the mixed diet, repeated measures analysis of body mass was carried out for the full experimental period. The duration of the instars and the "weight at molt" were analyzed with one-way ANOVA. The data were transformed when the assumption of homogeneity of variance was not met (for details, see Results). Post hoc mean comparisons between treatments were done with Student's t-test. Furthermore a two-way ANOVA was used to test for any interaction between sex and treatment on development. All statistical analyses were performed with JMP 5.0 for windows (SAS institute).

RESULTS

**Survivorship.**—There was an overall significant treatment effect on survival (Log Rank test,  $\chi^2_5 = 78.7382$ ,  $P < 0.0001$ , Fig. 1). The pairwise comparisons separated treatments into three groups: *D. melanogaster* and the entomobryids were of the same high qual-

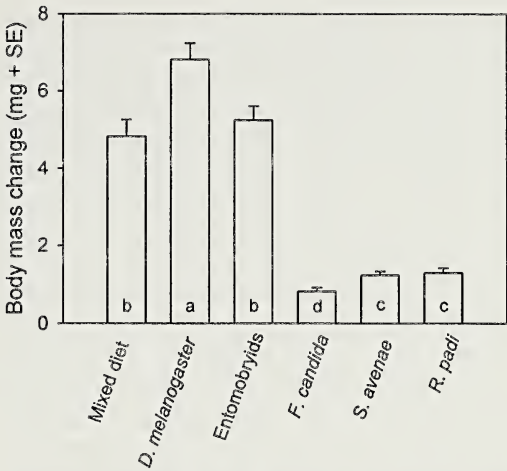


Figure 3.—Body mass change in the harvestman *Oligolophus tridens*, from the beginning of the experiment to week 3 (mg, mean + SE). Bars with different letters are significantly different (ANOVA, Student's t-test).

ity. The mixed diet was intermediate and the two aphids and *F. candida* were of low quality. Four individuals from the *F. candida* diet survived to the end of the experiment. None of the aphid-fed harvestmen survived.

**Growth.**—For the first three weeks there was a significant overall time \* diet interaction on the body masses (MANOVA,  $n = 86$ , Wilk's  $\lambda = 0.1355$ ,  $F = 15.2856$ , NumDF = 15, DenDF = 215.73,  $P < 0.0001$ , Fig. 2). The ranking of the diets was: *D. melanogaster* > entomobryid = the mixed diet >> the two aphid diets > *F. candida*. This is supported by an ANOVA test on the body mass change over the first three weeks of the experiment (overall ANOVA test on ln-transformed data,  $n = 86$ ,  $F_{5,80} = 94.9672$ ,  $P < 0.0001$ , Fig. 3). The repeated measures test was also done for the first three weeks on the animals that matured (from the treatments *D. melanogaster*, entomobryids and mixed diet), with both treatment and sex as factors. The test showed that there was no significant time \* diet \* sex interaction on the body mass (MANOVA,  $n = 53$ , Wilk's  $\lambda = 0.9305$ ,  $F = 0.5502$ , NumDF = 6, DenDF = 90,  $P < 0.77$ ). There was a significant time \* diet interaction on the body mass among the females from the high-quality treatments over all 10 weeks of the experiment (MANOVA,  $n = 26$ , Wilk's  $\lambda = 0.0528$ ,  $F = 4.6934$ , NumDF = 20, DenDF = 28,  $P < 0.0001$ ). Contrast tests showed that

the three diets all differed in body mass over time ( $P < 0.006$ ), though *D. melanogaster* and mixed diet ended up at the same level. If males were included in the test there was a significant time \* diet \* sex interaction on the body mass over 10 weeks (MANOVA,  $n = 53$ , Wilk's  $\lambda = 0.2133$ ,  $F = 4.4273$ , NumDF = 20, DenDF = 76,  $P < 0.0001$ ).

**Development.**—The harvestmen were in the second instar at collection. The maturation success was high on the *D. melanogaster* (95%), and the entomobryid (100%) diets, and the majority of harvestmen from the mixed diet matured (67%). Development was restricted on the aphid and *F. candida* diets and many of the harvestmen on these diets never molted. None of the harvestmen fed aphids molted to the fifth instar and only 19% from the *F. candida* diet matured. Generally the harvestmen from the *D. melanogaster* and mixed diet were the fastest to complete an instar and harvestmen from the *F. candida* treatment were the slowest (Fig. 4, right column). The total number of days from collection to the last molt showed a significant effect of diet (ANOVA test on ln-transformed data,  $n = 58$ ,  $F_{3,54} = 58.2450$ ,  $P < 0.0001$ ). The harvestmen from the *D. melanogaster* diet were the first to complete their development ( $39.0 \pm 0.68$  days, mean  $\pm$  SE), mixed diet and the entomobryid took a few days more ( $41.1 \pm 0.62$ ;  $43.6 \pm 0.86$ ) and those from *F. candida* were the last ( $68.5 \pm 3.06$  days). As to the "weight at molt", the *D. melanogaster* and entomobryid diets resulted in the heaviest animals and the *F. candida* diet resulted in a low body mass, which is particularly evident at the last molts (Fig. 4, left column). Both male and female data are included in Fig. 4. After five weeks the sex of the surviving harvestmen became apparent. The males reached a body mass of approximately 17 mg which was maintained with minor fluctuations (Fig. 2). The females increased their body mass considerably after maturation. A two-way analysis of variance was used to test for any sex-specific growth patterns (only the animals that matured from the treatments: *D. melanogaster*, entomobryids and mixed diet). There was no interactions (treatment \* sex,  $P > 0.11$ ), but there were significant effects of sex on the duration of instar 2, 5 and 6; and on the weight at the 6th molt (Table 1).

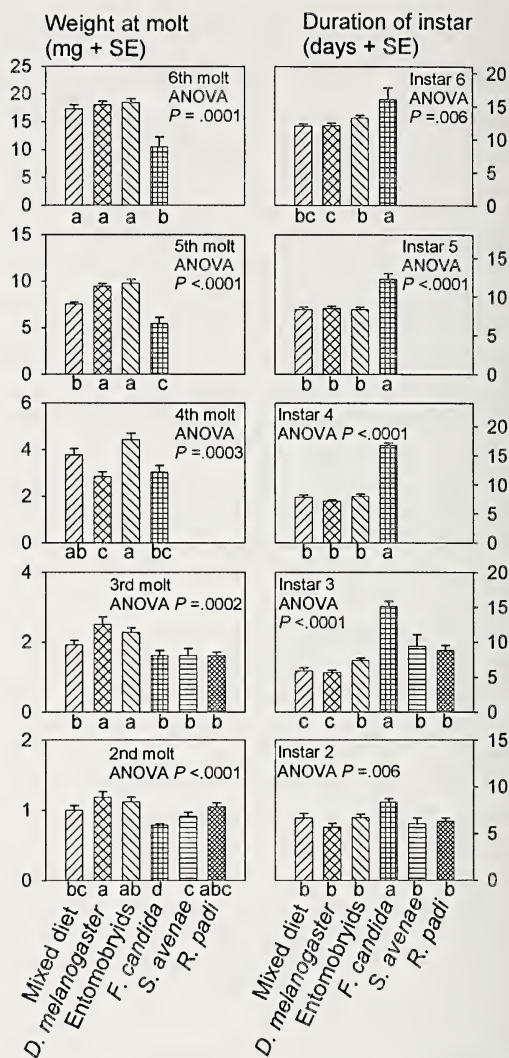


Figure 4.—Weight at molt (mg, mean + SE) and duration of instars (days, mean + SE) of harvestmen, *Oligolophus tridens*, reared on six diets. The dataset were tested with ANOVA, data were transformed if necessary. Overall  $P$ -values indicate significance. Pair wise comparisons were made with Students  $t$ -test; bars with different letters are significantly different. Male and female data are pooled in the figures.

## DISCUSSION

When the three fitness parameters, survival, growth and development are combined, the overall conclusion is that the diets separate in three different quality levels. The two aphids, *S. avenae* and *R. padi*, and the springtail *F. candida* were low-quality diets; both diets affected survival and growth. The development of the harvestmen was slow on the *F. candida*



diet, whereas harvestmen on the two aphid diets were only slightly slower than from the high-quality diets. Overall the mixed diet was of intermediate quality. It was of high quality regarding growth and development. Among the small juvenile harvestmen, the mixed diet caused a high mortality, an effect not seen in older animals. *Drosophila melanogaster* and entomobryids were high-quality prey, with respect to all three parameters. These results agree in general with the findings of other studies of generalist predators. *Drosophila melanogaster* and entomobryids have been reported to be of high quality to spiders (Toft & Wise 1999a; Mayntz & Toft 2001). Aphids are usually found to be of low quality to spiders (Toft 1995, 2000) and beetles (Bilde & Toft 1999), and *F. candida* was classified as a toxic prey to wolf spiders (Toft & Wise 1999a). A pronounced sexual size dimorphism was detected in the present experiment. The growth of the males stopped when the males were subadult, whereas the females gained body mass throughout the experiment and became much larger than the males. A large body mass is more important for females than for males, because females invest more in reproduction. The result of this fecundity selection is that females often are larger than males in invertebrates (Head 1995). The females in this experiment were generally faster to complete an instar and they reached maturity about 3 days before the males.

In a study on linyphiid spiders, Toft (1995) found that when the females were fed normal fruit flies, the hatching success of the spider eggs was high for the first two or three egg sacs, but then the hatching success declined. The quality of fruit flies can be improved by enrichment of the media with extra proteins, for example by adding dog food (Mayntz & Toft 2001). However, even a fruit fly diet, with or without enrichment, has its restrictions. Although it was the best prey of the study, protein enriched fruit flies was not fully sufficient for a wolf spider, as mortality and molting failures were higher than expected (Mayntz & Toft 2001). In the present study, mortality was low on the fruit fly diet and there were apparently no molting failures.

The effects of mixed diets are varied. Some studies have shown that dietary mixing is beneficial and essential to survival and development (Lowrie 1987; Uetz et al. 1992), others

that it depends on what the mixed diet consists of, i.e. it has to be the right mix (Marcussen et al. 1999; Toft & Wise 1999a). In this study the mixed diet caused a high mortality at the beginning, which might be due to the low-quality parts of the diet, i.e., *F. candida* and the aphids. If low-quality and potentially toxic prey comprise a large part of the diet, a mixed diet may not be beneficial. Those that survived the first few weeks may either have had a physiological tolerance to the low-quality prey or been able to reject them. If the surviving harvestmen in the mixed diet group developed an increased preference for the high-quality prey, their diet basically consisted of a mix of two high-quality preys. If high-quality prey is provided, there might be no or even negative effects of adding other prey types. In this study it seems that a monotonous high-quality diet, as for example *D. melanogaster* or the entomobryids, is better than a mixed diet of high-quality and low-quality or potentially toxic elements.

In this experiment the *F. candida* diet was of low quality to the harvestmen, both regarding survival, growth and development. Some of the harvestmen from the *F. candida* treatment survived, gained weight and molted to maturity. This shows that they did eat *F. candida* and that some of the harvestmen must have been more tolerant to the potentially toxic components in this diet than others. *Folsomia candida* is toxic to spiders, as spiders fed *F. candida* died faster than starved controls (Toft & Wise 1999a) and they cannot complete their development on a diet of pure *F. candida* (Fisker & Toft 2004); furthermore *F. candida* induced a specific feeding aversion in a spider (Toft & Wise 1999b). It was therefore a surprise that some of the harvestmen in the present experiment survived and developed. This could indicate genetic variation in the ability to cope with the toxic collembolan (cf. Beck & Toft 2000). It is possible that at least some of the harvestmen are better able to overcome the chemical defenses in *F. candida* than the spiders are. The harvestman *Mitopus morio* (Fabricius 1799) can tolerate the defensive alkaloids of their leaf beetle prey, by avoiding bioactivation and by rapid elimination of the detoxification products via the feces (Hartmann et al. 2003). Perhaps a similar process is operating in *O. tridens*, but with a high variation in individual ability to tolerate

Table 1.—Weight at molt (mg, mean  $\pm$  SE) and duration of instar (days, mean  $\pm$  SE) in male and female *Oligolophus tridens* from the treatments: *Drosophila melanogaster*, entomobryids and mixed diet. Only animals that matured are included in the tests. Welch ANOVA was used if the assumption of homogeneity of variance was not met. Asterisks indicate level of significance (\* $P$  < 0.05, \*\* $P$  < 0.01, \*\*\* $P$  < 0.001).

	Weight at molt (mg)			Duration of instar (days)		
	♂	♀		♂	♀	
2nd molt/instar 2	1.09 $\pm$ 0.06	1.16 $\pm$ 0.07	—	7.15 $\pm$ 0.33	5.74 $\pm$ 0.34	**
3rd molt/instar 3	2.24 $\pm$ 0.15	2.26 $\pm$ 0.15	—	6.40 $\pm$ 0.30	6.23 $\pm$ 0.31	—
4th molt/instar 4	3.72 $\pm$ 0.22	3.67 $\pm$ 0.23	—	7.59 $\pm$ 0.25	7.71 $\pm$ 0.26	—
5th molt/instar 5	9.13 $\pm$ 0.28	8.80 $\pm$ 0.29	—	8.68 $\pm$ 0.22	7.99 $\pm$ 0.22	*
6th molt/instar 6	16.65 $\pm$ 0.50	19.42 $\pm$ 0.53	***	12.92 $\pm$ 0.31	11.86 $\pm$ 0.32	*

*F. candida*. It is possible that freeze-killing of the prey, as used in this study, can alter the chemical composition, compared to live animal prey. However, a study of the carabid beetle *Bembidion lampros* (Herbst) showed that freeze-killing did not change the palatability of the springtails used as food (Bilde et al. 2000).

The few harvestmen fed *F. candida* that survived and matured obtained a lower body mass compared to the harvestmen from the other three diets. It is possible that *F. candida* contains toxic substances that impede development. In a study of a linyphiid spider it was suggested that *Folsomia fimetaria* (Linnaeus) "contains an element that inhibits digestion" (Marcussen et al. 1999). A similar result was seen in a study of a wolf spider (*Pardosa prativaga*) in which *F. candida* apparently inhibited the utilization of a better quality prey (*D. melanogaster*) (Fisker & Toft 2004). *Pardosa prativaga* compensated for the toxic effect of *F. candida* by increasing the intake of *D. melanogaster*, but the spiders still showed a higher mortality and grew more slowly than spiders fed only *D. melanogaster* (Fisker & Toft 2004). If the harvestmen on the mixed diet ate *F. candida*, they might have been exposed to toxins that decrease the digestion and/or utilization of the high-quality parts of the diet, and thereby caused a high mortality in the first few weeks. The high early mortality in the mixed diet and in the *F. candida* diet can also be explained by the size of the harvestmen. Studies have shown that small juvenile wolf spiders are more dramatically affected by *F. candida* than are larger juveniles

(Toft & Wise 1999b; Fisker & Toft 2004). This also seems to be the case for harvestmen.

Low ranking of aphids as food is widespread among generalist predators (Bilde & Toft 1994, 1999; Toft 1995). This experiment shows that *O. tridens* cannot survive on a pure aphid diet. High mortality was also the result in an experiment with larvae of the staphylinid beetle *Tachyporus hypnorum* (Fabricius) (Kyneb & Toft 2004). Aphids can also affect development. Wolf spiders (*Pardosa amentata* (Clerck 1757)) were unable to go through the first molt, and all the spiders died within two weeks, when fed a pure aphid diet (Toft 1995). These studies also indicate a limitation on the quantity of aphids the spiders and beetles can tolerate (Bilde & Toft 1994; Toft 1995). The food consumption was not measured in the present experiment, but it is very likely that the harvestmen consumed considerably fewer aphids than fruit flies. The prey in this study was freeze killed, before being offered to the harvestmen. This process neutralized the siphuncular defense system of the aphids, making predation easier (Toft 1995). The low quality of the aphid diet must therefore rely on a deterrent or toxic substance in the aphids which prevents the harvestmen from utilizing the nutrients. Dixon & McKinlay (1989) studied aphid predation by harvestmen in a potato field. They state that opilionids have been neglected and probably undervalued as predators of crop pests. A microcosm study with *R. padi* and different generalist predators showed that *O. tridens* was the most efficient predator; reducing aphid numbers up to 97% as compared to predator-free controls (Madsen et al. 2004).



These studies of aphids and harvestmen are in contrast to our results, from which it seems unlikely that harvestmen, at least not *O. tri-dens*, can act as a powerful biocontrol agent. Harvestmen may, however, contribute to the combined effect of the generalist predator complex on aphid population growth (Symondson et al. 2002).

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## CHROMOSOMAL DATA OF TWO PHOLCIDS (ARANEAE, HAPLOGYNAE): A NEW DIPLOID NUMBER AND THE FIRST CYTOGENETICAL RECORD FOR THE NEW WORLD CLADE

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**ABSTRACT.** *Mesabolivar luteus* (Keyserling 1891) and *Micropholcus fauroti* (Simon 1887) specimens were collected in Ubatuba and Rio Claro, both in the state of São Paulo, Brazil. *Mesabolivar luteus* showed  $2n (\delta) = 15 = 14 + X$  and  $2n (\text{♀}) = 16 = 14 + XX$  in mitotic metaphases and  $7\text{II} + X$  in diplotenic cells. During late prophase I, all bivalents presented a ring shape, evidencing two chiasmata per bivalent. In this species, some diplotenic cells appear in pairs, maybe due to specific characteristics of the intercellular bridges. The metaphases II showed  $n = 7$  or  $n = 8 = 7 + X$  chromosomes. *Micropholcus fauroti* evidenced  $2n (\delta) = 17 = 16 + X$  in spermatogonial metaphases and  $8\text{II} + X$  in diplotenic cells, with only one chiasma per bivalent, contrasting with *M. luteus*. In both species, all chromosomes were metacentrics. The sexual chromosome X was the largest element and appeared as a univalent during meiosis I. These are the first cytogenetical data for the genera *Mesabolivar* and *Micropholcus*. Additionally, *M. luteus* is the first chromosomally analyzed species of the New World clade and the observed diploid number for *M. fauroti* had not yet been recorded in Pholcidae.

**Keywords:** Arachnida, Meiosis, chromosomal morphology, spider, diplotene pair

Pholcids are small to medium sized spiders, with total length ranging from 1–15mm, usually with six or eight eyes, and legs several times longer than the body length. Specimens are found in low and high elevations, forests and deserts, leaf litter and tree canopies. There are several synanthropic species with cosmopolitan distribution. These characteristics taken together make the family Pholcidae Koch 1851 the most diverse among the haplogyne group, comprising 75 extant genera and 866 extant species (Huber 2000, 2005).

According to the cladogram proposed as a working hypothesis by Huber (2000) for the New World pholcids, the family is strongly supported as a monophyletic group and is divided into four clades: “ninetines”, “pholcines” (*Metagonia* Simon 1893 + *Pholcus* group sensu Huber, 1995), “holocnemines” (*Holocnemus* group sensu Timm, 1976 + *Artema* Walckenaer 1837 + *Physocylus* Simon 1893 + *Priscula* Simon 1893) and “New

World clade”. The latter includes most of the genera and is the only one that is exclusive for the New World. However, Huber (2000) himself pointed to “ninetines” and “holocnemines” as questionable monophyletic groups.

Despite the high number of Pholcidae species, only nine species (1%) of five genera have been chromosomally analyzed, i.e., “pholcines”: *Pholcus crypticolens* Bösenberg & Strand 1906,  $2n (\delta) = 24 = 22 + X_1X_2$  (Suzuki 1954); *Pholcus manuei* Gertsch 1937 (under *Pholcus affinis* Schenkel 1953),  $2n (\delta) = 25 = 24 + X$  (Wang et al. 1997); *Pholcus phalangioides* (Fuesslin 1775),  $2n (\delta) = 24 = 22 + X_1X_2$  (Rodríguez-Gil et al. 2000) and *Spermophora senoculata* (Dugès 1836) (under *Spermophora meridionalis* Hentz 1841, misspelled as *Spermaphora meridionalis*),  $2n (\delta) = ? = ? + X_1X_2$  (Painter 1914), and “holocnemines”: *Artema atlanta* Walckenaer 1837 (misspelled as *Artema atlenta*),  $2n (\delta) = 32$

$= 30 + X_1X_2$  (Parida & Sharma 1987; Sharma & Parida 1987); *Crossopriza lyoni* (Blackwall 1867),  $2n(\delta) = 27 = 26 + X$  (Bole-Gowda 1958),  $2n(\delta) = 25 = 24 + X$  (Srivastava & Shukla 1986),  $2n(\delta) = 24 = 22 + X_1X_2$  (Sharma et al. 1959) and  $2n(\delta) = 23 = 22 + X$  (Parida & Sharma 1987; Sharma & Parida 1987); *Physocyclus californicus* Chamberlin & Gertsch 1929,  $2n(\delta) = 15 = 14 + X$  (Cokendolpher 1989); *Physocyclus enaulus* Crosby 1926,  $2n(\delta) = 15 = 14 + X$  (Cokendolpher 1989) and *Physocyclus* sp.,  $2n(\delta) = 15 = 14 + X$  (Cokendolpher & Brown 1985; Cokendolpher 1989). In the species whose chromosomal morphology has been determined, all chromosomes are metacentric, with the exception of the  $X_1$  and  $X_2$  chromosomes of *C. lyoni* described by Sharma et al. (1959) and *P. crypticolens*, which are acrocentric. There are no cytogenetical data on "ninetines" and "New World clade".

The genus *Mesabolivar* González-Sponga 1998, included in the New World clade by Huber (2000), includes 34 species from which 24 occur in Brazil (Huber 2005). This genus arises as a sister group of *Coryssocnemis* Simon 1893; however, this position is not yet clearly established. The genus *Mesabolivar* has been divided into four "operational" groups, based on morphological characters: a "northern group with spines on male metatarsi" (5 species), a "northern group without spines on male metatarsi" (6 species), a "southern/eastern group" (15 species) probably not monophyletic, and a "miscellaneous group" (7 species), certainly polyphyletic, that will probably be partly transferred to other genera/group (Huber 2000).

*Mesabolivar luteus* (Keyserling 1891) is a species belonging to the "miscellaneous group," probably related to *Mesabolivar levii* Huber 2000, and is distributed in the states of Rio de Janeiro, São Paulo, Paraná and Rio Grande do Sul, in Brazil. The genus *Micropholcus* Deeleman-Reinhold & Prinsen 1987 (pholcine) includes only two species, of which only the Pantropical species *Micropholcus fauroti* (Simon 1887) occurs in Brazil by introduction and lives as a synanthropic species (Huber 2000).

The use of chromosomal data in phylogenetic analysis is relatively new, and the criteria to codify these data are controversial (Modi 1987; Borowik 1995). Additionally, cy-

togenetic analysis may have some difficulties when compared with other kinds of analysis: the specimens must be kept alive until the slide preparations, some of them do not have cell division at the moment of analysis, and some techniques are expensive. Nevertheless, chromosomal data have a potential usefulness for phylogenetic inference, because they are heritable, homologue states can be identified, and the characters are independent from each other (Borowik 1995). Basically, a chromosomal phylogeny can be constructed based on the minimum number of rearrangements required or the maximum number of shared segments (Rokas & Holland 2000). Although chromosomal data has not been used for cladistic analysis in spiders, there have been some attempts in other groups, such as mammals, to obtain characters by conventional (Nagamachi et al. 1999; Garcia et al. 2000) or molecular cytogenetic techniques (Oliveira et al. 2002).

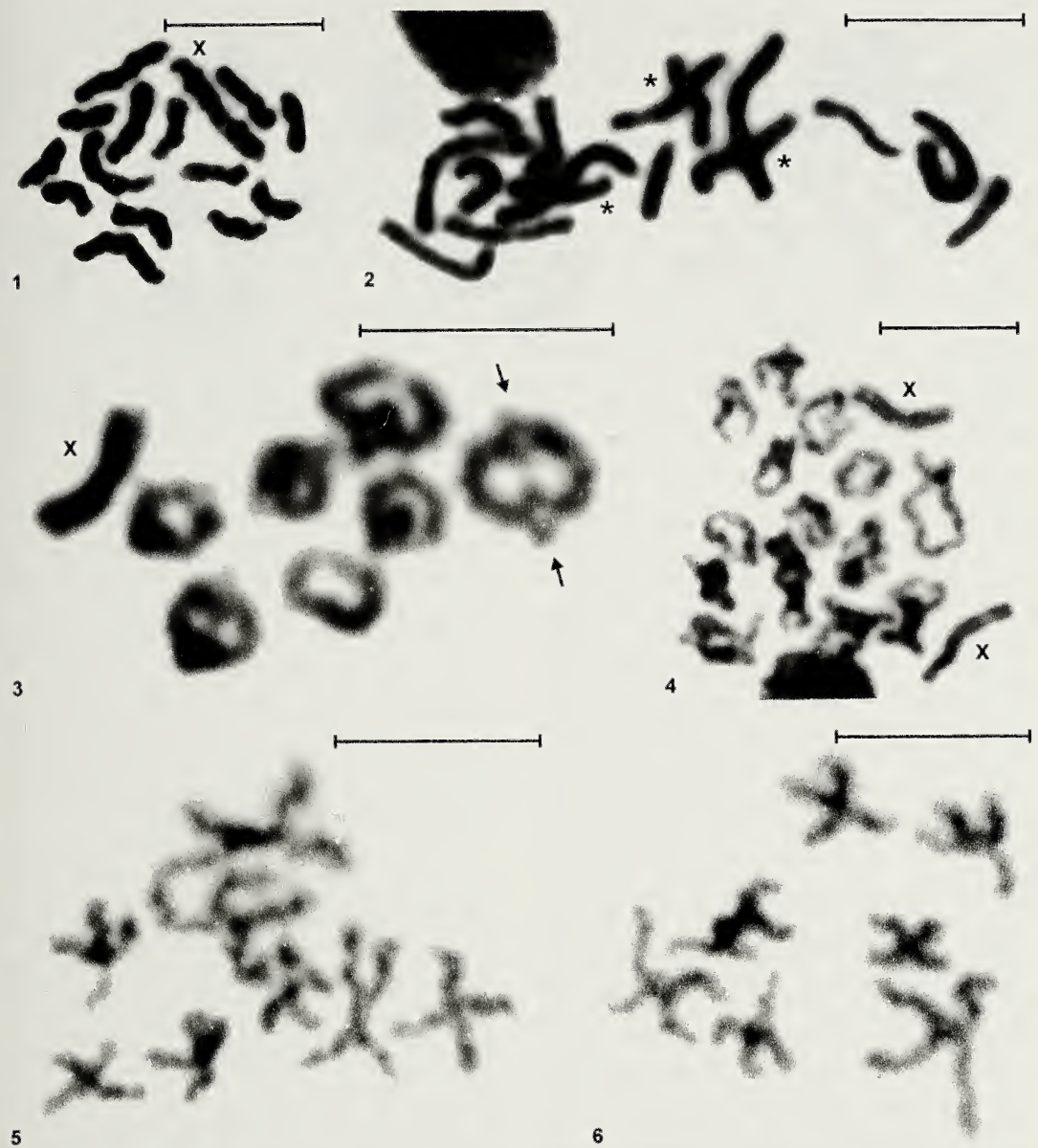
The aim of this study is to characterize the chromosomes of the species *M. luteus* and *M. fauroti*, analyzing standard stained mitotic and meiotic cells, in order to begin an effort to establish karyotypic relationships among species in the Pholcidae.

## METHODS

Three males and one female of *M. luteus* were collected at Maranduba beach, Ubatuba (23°43'S 45°07'W), and five males of *M. fauroti* were collected in buildings in Rio Claro and Ubatuba (22°41'S 47°56'W and 23°43'S 45°07'W), both in the state of São Paulo, southeastern Brazil. The specimens are deposited in the collection of the Laboratório de Artrópodes Peçonhentos, Instituto Butantan, São Paulo (IBSP, A.D. Brescovit) under the numbers IBSP 42785 (*Mesabolivar luteus*), 42782, 42783, 42784, 47504 and 47505 (*Micropholcus fauroti*).

Gonads were dissected in Ringers solution for insects, transferred to colchicine solution (0.16% in Ringer for insects) and left for 2 hrs.; a volume of hypotonic solution (tap water) equal to that of the colchicine solution was added and after 15 mins. the material was placed in Carnoy I fixative solution for 60 min., after which it was macerated in 60% acetic acid on the surface of the slide. The slide was dried on a metal heating plate (35–40 °C) and stained with a 3% Giemsa solution





Figures 1-6.—*Mesabolivar luteus* cells. 1. Spermatogonial metaphase, with  $2n = 15 = 14 + X$ . 2. Oogonial metaphase, with  $2n = 16 = 14 + XX$ . The asterisks indicate overlapped chromosomes. 3. Diplotene, with  $7II + X$ . Arrows indicate the chiasma location. 4. Diplotene nuclei, constituting a pair of cells. 5. Metaphase II, with  $n = 8 = 7 + X$ . The X could not be identified in this spread. 6. Metaphase II, with  $n = 7$ . Scale = 10  $\mu m$ .

for 13-15 min. The cells were photographed under a Zeiss microscope and the chromosome morphology classification was determined according to Levan et al. (1964). The number of analyzed chromosomal spreads was 65 for *M. luteus* and 40 for *M. fauroti*. In each of these spreads, the chromosome number was

determined and no intraspecific variation was detected.

RESULTS

*Mesabolivar luteus*.—The mitotic metaphases showed  $2n = 15 = 14 + X$  in males (Fig. 1) and  $2n = 16 = 14 + XX$  in females



Figures 7–8.—*Micropholcus fauroti* cells. 7. Spermatogonial metaphase, with  $2n = 17 = 16 + X$ . 8. Diplotene, with  $8II + X$ . Arrow indicates a terminal chiasma and arrowhead points to an interstitial chiasma. Scale =  $10\ \mu\text{m}$ .

(Fig. 2). In the spermatogonial metaphases, the X chromosome is always easily identified as the largest element (Fig. 1). The chromosomal morphology is not clear in the mitotic metaphases due to the low degree of chromosome condensation. Diplotene cells showed  $7II + X$  (Fig. 3). All bivalents present a ring shape, evidencing the occurrence of two terminal chiasmata per bivalent, and the X chromosome constitutes an univalent during all meiosis I (Fig. 3). Some diplotene cells appeared in pairs (Fig. 4). Metaphases II showed  $n = 8 = 7 + X$  (Fig. 5) or  $n = 7$  (Fig. 6) chromosomes. The X chromosome cannot be recognized in the  $n = 8$  cells due to the irregular chromosome appearance. Despite the low staining contrast, the chromosomal morphology of this species was determined as metacentric.

***Micropholcus fauroti*.**—The spermatogonial metaphases showed  $2n = 17 = 16 + X$  (Fig. 7). The largest chromosome of complement is X, which is easily identified in all analyzed metaphases (Fig. 7). Despite the low staining contrast and the low morphology resolution, the chromosomes seem to be biarmed (Fig. 7). Diplotene cells possessed  $8II + X$  (Fig. 8) and each bivalent shows only one chiasma, terminal or interstitial (Fig. 8). The X chromosome appears as a univalent during meiosis I (Fig. 8).

#### DISCUSSION

Despite high diversity of pholcid species among haplogynes, this family is poorly known from the cytogenetic point of view. This could be due to the lack of Pholcidae

cytogenetic researchers, the relatively small size of pholcid species and their chromosomes, and the difficulty in obtaining good quality chromosomal preparations.

As the generic name suggests, *Micropholcus fauroti* is a very small spider, 1–2mm in length. Thus, dissection of the specimens, as well as the removal of the testis, is very difficult. Additionally, only one slide, with few cells, can be obtained per specimen due to extremely minute size of the testis.

In relation to the chromosome length, Painter (1914), Suzuki (1954) and Bole-Gowda (1958) emphasized the very small size of the elements. The largest chromosome of *P. crypticolens*, obtained by Suzuki (1954), measured only around  $2.4\ \mu\text{m}$ . The largest chromosome of *C. lyoni* is the X chromosome, which measures  $5.8\ \mu\text{m}$ , but the largest autosome measures only around  $2.3\ \mu\text{m}$  (Bole-Gowda 1958). The measurements of the largest chromosomes of *M. luteus* and *M. fauroti* were respectively 9 and  $7\ \mu\text{m}$  (for the X chromosome), and 6 and  $5\ \mu\text{m}$  (for the autosomes). Thus, the chromosomes of the studied species are not as small as those obtained by Suzuki (1954) and Bole-Gowda (1958). On the other hand, they are not as large as those of other haplogyne genera, such as *Loxosceles* Heineken & Lowe 1832 (Sicariidae) in which the largest chromosomes measure around  $15\ \mu\text{m}$  (Silva et al. 2002).

Concerning the preparation quality, Painter (1914) and Suzuki (1954), using different types of fixative solutions, called attention to the unfavorable fixation of pholcid chromo-



somes. A similar problem occurred with *M. luteus* and *M. fauroti* chromosomes, when Carnoy I fixative solution was used, resulting in low staining contrasts. Alternative fixation methods should be tested in pholcid species.

*Mesabolivar luteus* is the first cytogenetically studied species from the "New World clade" and showed a diploid number equal to that found in three *Physocyclus* species (holcnemines) analyzed by Cokendolpher (1989), despite the fact that these genera belong to different clades. Thus, the  $2n = 15$  could have arisen independently at least two times within the pholcids. *Micropholcus fauroti* is the first cytogenetically analyzed species from this genus and until now, its diploid number had not yet been recorded in Pholcidae. The presence of binned chromosomes in both species of this study is a feature shared among most of the haplogyne group species, as stated by Rodríguez-Gil et al. (2002).

In both species, the largest chromosome of the complement is the X chromosome. This is in agreement with the data obtained by Bole-Gowda (1958) for *C. lyoni* and by Cokendolpher (1989) for three *Physocyclus* species. During interphase, the observed X chromatin positive heteropycnosis of *M. fauroti* is similar to that recorded for *C. lyoni* by Bole-Gowda (1958).

The studied species showed significant differences from each other in relation to the chiasma number, during meiosis. However, information on chiasma number and position was not provided by previous papers on pholcid cytogenetics. Thus, these characteristics cannot be used as parameters to compare related species or to establish a pattern within the pholcid groups.

The diplotene pairs found in *M. luteus* are probably a consequence of the germ cell arrangement and interaction, which constitute "cysts" with synchronously dividing cell connections via intercellular bridges due to the lack of cytokinesis during spermatogenesis. Alberti & Weinmann (1985) described the presence of similar cysts in the testis of *P. phalangiodes*.

In relation to these grouped cells, two questions are crucial: why do they appear in pairs and not in larger groups of cells; and why do these pairs only appear in the diplotene phase? Concerning the first question, Pepling & Spradling (1998) have verified a tendency towards

the increase in number by the power of two in mouse embryo oogonial mitotic cells, being more frequently found in clusters of two cells. Clusters with more cells are probably more susceptible to breaks during slide preparation. However, the possibility of finding such clusters in future analysis cannot be discarded. With respect to the second question, this feature is probably a consequence of the skewed cellular phase ratio in the sample, because from the 105 spreads obtained, only 9 were mitotic metaphases and the others were almost all diplotenes. Possibly, paired mitotic metaphases should be also found in *Mesabolivar luteus*. An ultrastructural analysis of spermatogenesis would be of interest to answer these questions. Additionally, further analysis of other pholcid species is needed to verify whether this pairing of cells also occurs.

The possibility of the occurrence of polyploidy in *M. luteus* was discarded, at least in the first instance, due to two main reasons: the lack of polyploid metaphase II cells (despite the low frequency of cells in this meiotic stage) and the lack of tetravalents or chromosomal chains at meiosis I. The formation of chromosomal chains is not a strict rule in polyploids, but they are frequently observed (John 1990).

The cytogenetic analysis of the pholcines *Leptopholcus* Simon 1893 and *Metagonia* Simon 1893, and of the holcnemines *Smeringopus* Simon 1890, *Holcnemus* Simon 1873 and *Priscula* Simon 1893 seems to be extremely important to establish the karyotypic evolution in these two clades. The cytogenetical study of the ninetines and of the New World clade requires more exhaustive research, considering that only *Mesabolivar* was analyzed and that there are numerous genera belonging to these two clades. Finally, when a full cytogenetical data set becomes available for Pholcidae, it could be used to improve the proposed phylogenetic hypothesis for the family.

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## SIX STRIDULATING ORGANS ON ONE SPIDER (ARANEAE, ZODARIIDAE): IS THIS THE LIMIT?

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**ABSTRACT.** A new type of stridulatory organ is described and figured occurring in three species of *Mallinella* Strand from Thailand and Singapore. In one species there are four stridulatory organs, with the ridges on femora I and II and the pegs in the shape of granulations on femora II and III. In both the other species an additional pair occurs, with ridges on femora III and pegs on femora IV. To date no more than four stridulatory organs have been recorded on a single spider. Examples of various known forms of stridulatory organs on spiders are illustrated and their significance briefly discussed.

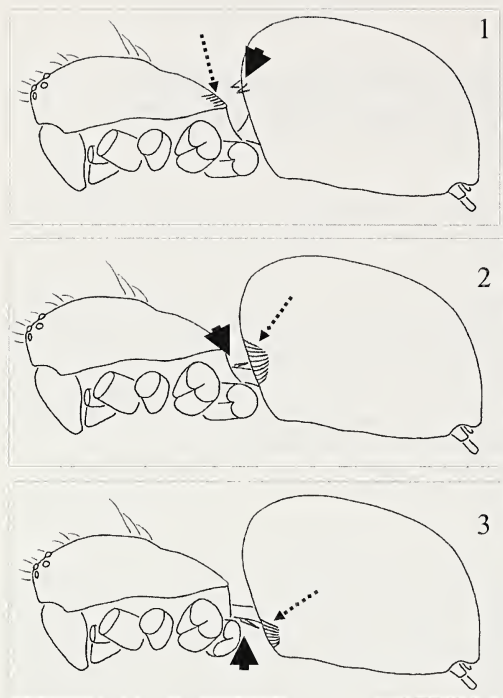
**Keywords:** Stridulation, Thailand, Singapore, courtship, mate check

Stridulating organs are manifold in spiders and were reported for at least 22 families of spiders in Uetz & Stratton (1982) and since then, several cases in other families (Corinnidae, Tetragnathidae, Zodariidae, see below) have been mentioned. Some of the organs are single, but paired stridulatory organs appear to occur more commonly. These organs inevitably comprise two elements: the “pars stridens”, a sclerotized area provided with a series of ridges referred to as “the file” or simply “the ridge” in those cases where there is only one, and the “plectron” which may be one or a series of stiff setae or pegs, sometimes called “the plectrum” or “the scraper” in the case of a single peg.

In single stridulatory organs, sounds are produced by rubbing the front of the abdomen against the rear of the cephalothorax, the surfaces of which are provided either with ridges, pegs or stiff setae (Figs. 1–3) (e.g. Maddison & Stratton 1988a, b). The same applies to the sound produced by files on the inner surface of the chelicerae that occurs in Mygalomorphae or on the inner surface of the anterior lateral spinnerets as found in some Theridiidae (Forster et al. 1990; Agnarsson 2004). Paired stridulatory organs, usually in the form of ridges and pegs, occur in many other taxa. Most commonly, these ridges occur on the chelicerae (externally), and are rubbed by the palps; on the booklung covers, rubbed by the fourth legs; or on the coxae of the first legs rubbed by a peg on the second trochanters (e.g. Hinton & Wilson 1970). Rovner (1975)

recorded a stridulatory device in males of *Lycosa* and *Schizocosa*: a plectrum on the male palpal tibia rubs against a file on the cymbium. Edwards (1982) later found a similar device in the salticid *Phidippus mystaceus* (Hentz). Legendre (1963) and Uetz & Stratton (1982) provided a fairly complete overview of the different types of stridulatory organs, summarized here in Figs. 1–10. Starck (1985) gave a complete list of the known stridulatory organs, analyzed the structure of the elements that compose a stridulating organ and discussed the function and the evolutionary aspects of the devices. He stressed the homoplasy of these structures in different taxa and concluded that there has been parallel development of similar organs, even within the same family.

Since these early papers, several more types of stridulatory organs have been described. Maddison (1987) found *Marchena minuta* (Peckham & Peckham 1888) and other jumping spiders (Salticidae) to be provided with ridges or a row of stout setae on the dorsal base of the femora I combined with respectively a row of setae or a stridulatory file on the carapace just under the eyes. Simon (1937) was apparently aware of this structure and mentions the femoral tubercles in *Icius* Simon. Wunderlich (1995) reported on an external longitudinal ridge on the chelicerae in *Zygiometella* Wunderlich (Tetragnathidae), supposedly combined with setae on the inner side of the male palp to form a stridulatory organ. Ramirez et al. (2001) found a similar



Figures 1–3.—Examples of spiders with one stridulatory organ (appendages omitted). 1. *Steatoda* Sundevall (Theridiidae), with file on carapace, pegs on abdomen; 2. *Cambridgea* L. Koch (Stiphidiidae), with file on abdomen, pegs on pedicel (dorsally); 3. *Cambridgea* L. Koch (Stiphidiidae), with file on abdomen, pegs on pedicel (ventrally) (after Legendre 1963 and Uetz & Stratton 1982). Dotted arrows = files and ridges, solid arrows = pegs.

stridulating system in *Olbus* Simon 1880 (Corinnidae): a retrolateral ridge on femur IV corresponding with a field of modified seta bases on the abdomen. This organ combines with a field of prolateral setae with modified bases on the prolateral side of the same femur opposed to a field of evenly spaced setae with transversely arranged bases. If both these combinations represent stridulating organs, this was the first case reported of four such organs in a spider.

Only one putative stridulating organ was so far reported in the Zodariidae: the species *Aktytara homunculus* (Jocqué 1991) has warts on the anterior surface of the abdomen corresponding with ridges on the posterior part of the carapace (Jocqué 1991).

The present paper reports on a remarkable case of multiple stridulatory organs and pro-

vides a concise overview of the present knowledge on these structures.

## METHODS

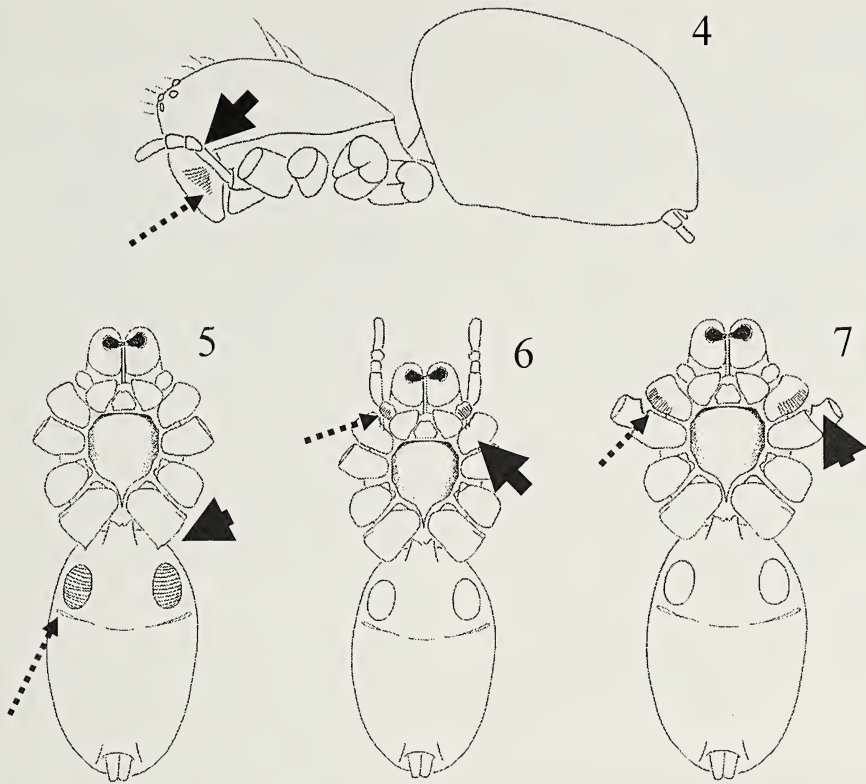
Stridulating organs on the femora of *Mallinella* Strand 1906 (Zodariidae) were noted for the first time while sorting through collections of representatives of the family from Thailand collected by P. Schwendinger. A dark area around the stridulating file of the species with four stridulating organs made that region conspicuous. Without the color contrast, the structures would probably have passed unnoticed. Stridulatory structures were found on the males of two species; each species was represented by only one male. A more interesting example was found in the collection of J. Murphy. This collection included both sexes of what appeared to be *M. cinctipes* (Simon 1892) according to the drawing of the epigyne in Workman (1896) and a photo of the spider by Koh (1989).

All the examined specimens belong to the palaetropical genus *Mallinella* that has a vast distribution from West Africa to northern Australia (Jocqué 1993). They are typical forest soil-dwellers and compulsory termite feeders that hide in silk-lined spherical buried retreats during daytime.

**Specimens examined.**—*Mallinella* sp. 1: 1♂ (with four stridulatory organs), Thailand, Penang Hill, 150–330 m, 02.xii.1991 (P. Schwendinger). *Mallinella* sp. 2: 1♂ (with six stridulatory organs), Thailand, Doi Chiang Dao, 510 m, 25.x–23.xi.1990 (P. Schwendinger). *Mallinella cinctipes*: 1♂: Singapore, Upper Pierce Reservoir, iii.1986 (Murphy collection 13418); 1♂: Singapore, Upper Pierce Reservoir, ii.1988 (Murphy collection 15443); 3♂, 1♀: Singapore, Bukit Timah, ii.1988 (Murphy collection 15471). The voucher specimens of the unknown species from Thailand shall be deposited in the Musée d'Histoire Naturelle de Genève, Switzerland. Males were preserved in ethanol 75% in the field and examined in the lab.

The male specimen from Penang Hill was scanned using a XL30 ESEM scanning electron microscope in wet mode with cooling cell that leaves the specimen undamaged. Images (Fig. 13) were taken of the entire specimen at different depths and composed into a single photomontage by using an analogue camera and composition software. (Automontage of





Figures 4–7.—Examples of spiders with two stridulatory organs (appendages omitted). 4. Linyphiidae, Hahniidae (and many other families), with file on chelicerae, pegs on palps; 5-. Linyphiidae, with file on abdomen (ventrally), pegs on leg IV; 6. Linyphiidae, with file on palps, pegs on coxae I; 7. Linyphiidae, with file on coxae I, pegs on trochanters II (after Legendre 1963).

Synoptics). Other SEM images were taken with a JEOL 6480LV.

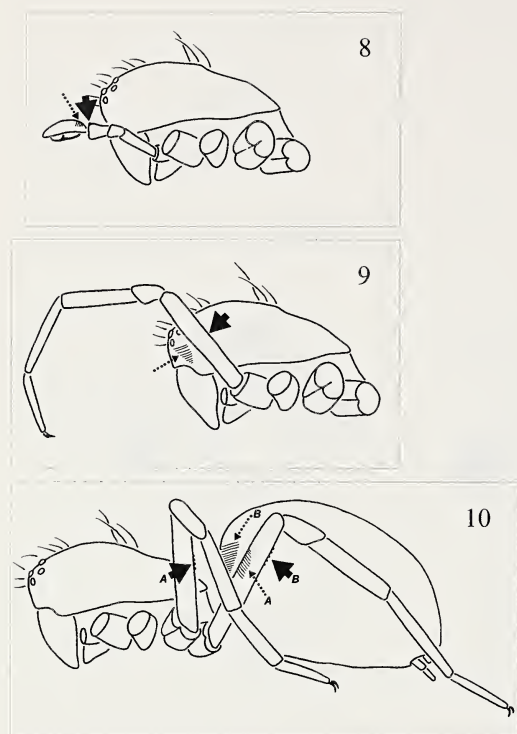
RESULTS

*Mallinella* sp. 1 (Figs. 11, 13) appears to have four and *Mallinella* sp. 2 and *Mallinella cinctipes* (Fig. 12) appear to have six stridulatory organs. In the latter, the ridges are situated on a conspicuous swelling (Figs. 15, 16) of the dorsal base of the anterior femora and are apparently rubbed by prolateral ventral granulations (Fig. 18) at the base of tiny setae on the following femur. In *Mallinella* sp. 1, the file area is rounded and has a diameter of 0.45 mm, with 48 ridges which means that the ridges are slightly less than 0.01 mm apart. The granulations are 0.045 mm apart. In *Mallinella* sp. 2 the ridges are somewhat thinner (52 in an area with diameter 0.41 mm) and the granulations more densely set at a distance of just under 0.01 mm. In *Mallinella cinctipes* the stridulation area on Fe II is on average

0.34 mm across and has 72 ridges which means that they are again thinner and about half as far apart as in the first species (5  $\mu$ m). The granulations are between 0.04 and 0.06 mm apart. The female of *M. cinctipes* has not the slightest indication of a femoral stridulation organ.

DISCUSSION

To date, no spider species with more than four stridulatory organs has been reported. The only probable case is that of *Olbus jaguar* Ramirez et al. 2001 mentioned in the introduction. As far as I am aware, no cases exist in which a single central stridulatory organ is combined with a symmetrical double organ. The number of stridulatory organs on a single spider is now known to be 1, 2, 4 or 6. The last two mentioned cases are especially surprising, as even in the case of other animals, such a high number has apparently never been recorded. The organ depicted here bears some



Figures 8–10.—8. Lycosidae, file on cymbium, peg on palpal tibia (after Rovner, 1975); 9. Salticidae, with file on side of carapace under the eyes, pegs on inner side of first femur (after Maddison, 1987). Dotted arrows = files and ridges, solid arrows = pegs; 10. Example of a spider with four stridulating organs and the only one known with a mixed set-up: *Olbus jaguar* (Corinnidae). One system (A) consists of a file on femur IV and pegs on femur III, the other one (B) of a file on the abdomen and pegs on femur IV (after Ramirez et al. 2001). Dotted arrows = files and ridges, solid arrows = pegs.

resemblance to those mentioned in *Olbus* and in *Marchena* Peckham & Peckham described by Maddison (1987) but in the zodariids the carapace and the abdomen are smooth and devoid of setae or ridges. In the *Mallinella*, the file is dorsolateral (Figs. 11, 12, 14–16) and directed towards the following femur with the granulations that apparently function as pegs. This is corroborated by the fact that the seta bases on the first femur (Fig. 17) have no granulate extensions whereas those of femora II, III and in some cases IV do (Fig. 18).

Stridulation may have two clearly different functions, i.e. defense and courtship (Starck 1985; Uhl & Schmitt 1996). Although there are no studies available for spiders with more

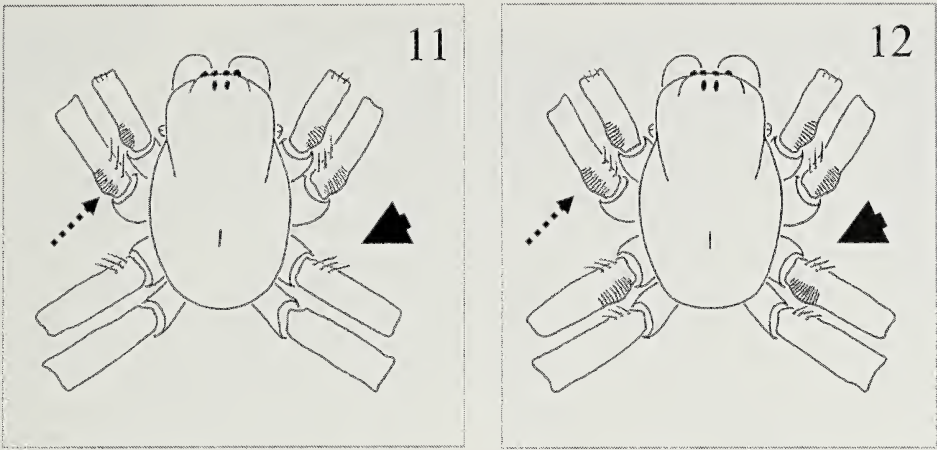
than two stridulatory organs, there is no reason to expect that the function should be different for multiple organs.

Defense stridulation in larger animals, such as mygalomorphs (Legendre 1963), is often audible to the human ear. However, in araneomorph spiders, stridulation probably originated as part of courtship (Starck 1985). Several hypotheses have been formulated regarding the function of this stridulation during courtship. These include mate recognition, antagonistic behaviour between males (Gwinner-Hanke 1970; Maddison & Stratton 1988a), stimulation of the female by the male (Eberhard 1996) and information transfer (Jocqué 1998). It is difficult to accept that more than one stridulating organ would be needed if the aim is to recognize the partner: the possibilities for variation with one “instrument” are endless and it is therefore unlikely that multiple stridulation organs are developed for that purpose. Stimulation of the partner is another possibility that has been invoked to explain the development of secondary sexual organs. The question always remains why species with similar morphology and life style would evolve such different degrees of partner stimulation.

“Mate check,” (Jocqué 1998, 2002) on the other hand, assumes that the quantity of information transferred during courtship is directly related to the ecological specialization of the species. Via an array of signals, combined in a so-called “mating module” (Jocqué 2001, 2002), the presence of crucial adaptations in the male mate is verified during courtship and mating. In the speciose genus *Mallinella*, species of which have a highly specialized biology, the development of a complex stridulatory apparatus as part of the mating module is a plausible explanation certainly because the females appear to be devoid of such organs.

Another fascinating question to be answered is how these stridulatory organs are operated. It is very unlikely and physically apparently impossible that they are all activated at the same time in an orchestra-like manner. It is therefore to be expected that the organs are activated consecutively and in pairs, one on either side of the animal. This prompts the question whether spiders with more than six stridulating organs can be expected. If the organs are arranged as in *Olbus jaguar* (see





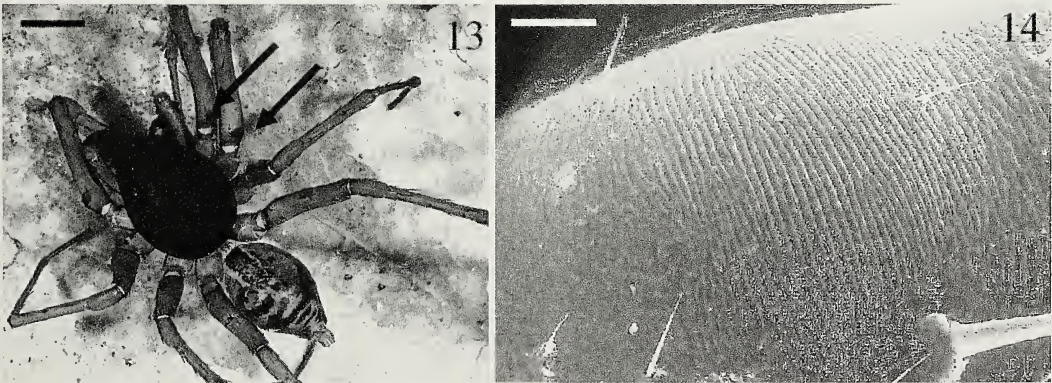
Figures 11–12.—Example of a spider with four and six stridulatory organs. 11. *Mallinella* sp. 1 (Zodariidae), with files on femora I and II, pegs on femora II and III; 12. *Mallinella* sp. 2 (Zodariidae), with files on femora I, II and III, pegs on femora II, III and IV. Dotted arrows = files and ridges, solid arrows = pegs.

above) a total of eight belongs to the possibilities. The arrangement in that species gives the impression that different types of stridulatory organs are present in one spider. Yet, as in the *Mallinella*, it can be expected that the movement involved is similar for both pairs: moving the femur with the pegs relative to the adjacent file. The main difference with the situation in *Olbus* is that in *Mallinella* the pegs are behind the file and it is difficult to imagine that a series of pegs would evolve on the abdomen. In *Olbus* it is the other way round and the last femur scratches a file on the abdomen. In this way it is possible to have four stridulating files on the same side operating them in sequence and with the same movement, like it must be the case for the organs in *M. cinc-*

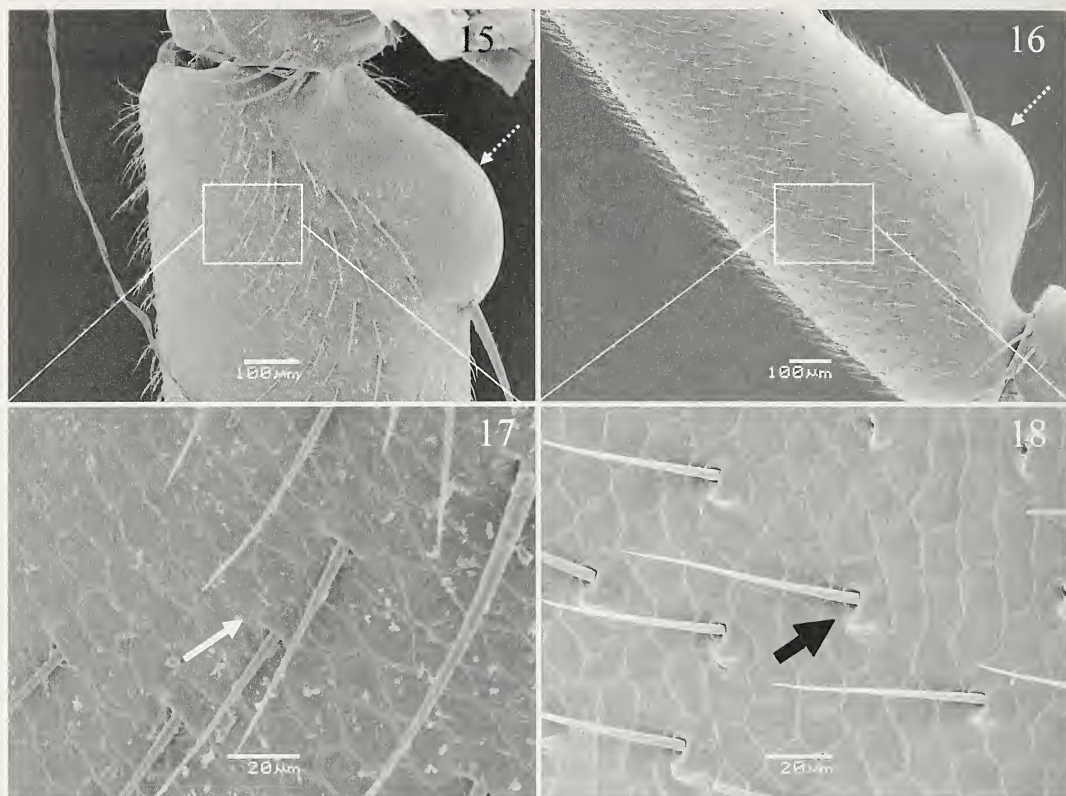
*tipes*. A spider with an eight instrument orchestra thus theoretically belongs to the possibilities.

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Figures 13–14.—*Mallinella* species 1 from Thailand ♂. 13, Habitus with arrows indicating files on femoral base I and II; 14, Stereoscan micrograph of femoral file. Scale bars = 1 mm (13); 0.1 mm (14).



Figures 15–18.—*Mallinella cinctipes* Singapore ♂. 15. Left femur I showing dorsal swelling with stridulating file (dotted arrow); 16. Right femur II showing dorsal swelling with stridulating file (dotted arrow); 17. detail of Fig. 15 showing knobless hair bases (white arrow); 18. detail of Fig. 16 showing pegs in the shape of a knob at hair base (solid black arrow).

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## FIRST ULTRASTRUCTURAL OBSERVATIONS ON THE TARSAL PORE ORGAN OF *PSEUDOCELLUS PEARSEI* AND *P. BONETI* (ARACHNIDA, RICINULEI)

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**ABSTRACT.** Due to their relative rareness and restricted distribution, little is known about the ultrastructure of ricinuleids. In particular, sense organs have not been the subject of electron microscopic research until now. Ricinuleids use their forelegs to explore their surroundings with tentative movements. The distal tarsomeres of legs I and II of two cavernicolous Mexican species, *Pseudocellus pearsei* from the Yucatán Peninsula and *Pseudocellus boneti* from Guerrero, were examined in this study with light microscopy, scanning (SEM) and transmission electron microscopy (TEM). A conspicuous feature of the distal tarsomeres of legs I and II is a single circular opening that extends as a deep tube-like pit into the tarsus. This pore organ is lacking in the 6-legged larvae. Comparable organs are present in Araneae, Scorpiones, Amblypygi and Anactinotrichida. The tarsal organs of the mentioned groups possess several types of sensilla (olfactory, thermo- and hygroresponsive and mechanosensitive). The pore organ is located in the distal third of the dorsal half of the tarsus. In longitudinal sections it shows a long oval shape. In cross sections it is nearly circular. The pore organ contains a large number of long, slightly curved setae. These setae are localized on the bottom and the lower two thirds of the wall of the pit and project into the lumen. The upper third of the wall is free of setae and shows folds which extend parallel to the opening. All setae inside the pit seem to be of the same type. In sections they show a complex inner structure and likely represent chemoreceptive wall pore single-walled (wp-sw) sensilla. This indicates a possible olfactory function. The pore organ is underlain by numerous gland cells which represent characteristics of unicellular “class I” gland cells.

**Keywords:** Tarsus, ultrastructure, sensory organs

The order Ricinulei Thorell 1892 is one of the smallest arachnid groups. Only 56 recent species, all belonging to the family Ricinoididae Ewing 1929, have been described. The recent species are divided into three genera. *Ricinoides* Ewing 1929 is from Western Central Africa, and *Cryptocellus* Westwood 1874 and *Pseudocellus* Platnick 1980 are both from Central America. Ricinuleids inhabit humid layers of soil and litter in tropical rainforests or caves (Cooke 1967; Mitchell 1970; Adis et al. 1989). They pass through 5 postembryonic life stages: a 6-legged larva, 3 nymphal stages (proto-, deuto- and tritonymph) and the adult stage (Mitchell 1970).

Most available studies about ricinuleids are taxonomic (Mitchell 1970). The knowledge about their internal morphology is based on

relatively few old fundamental studies (e.g., Hansen & Sørensen 1904; Millot 1945, 1949). Until recently, little has been known about the ultrastructure of ricinuleids as there have been few scanning and transmission electron microscopic studies on this animal group (for SEM see Legg 1976, 1977; Dumitresco & Juvara-Bals 1977; Platnick & Shadab 1976, 1977; Harvey 1984; Adis et al. 1999; for TEM see Alberti & Palacios-Vargas 1984; Ludwig & Alberti 1990; Ludwig et al. 1994). In particular, sensory organs have not been subjected to electron microscopic research until now. Ricinuleids use their forelegs, especially the elongated second leg, to explore their surroundings with tentative movements (Pollock 1967). Hence the presence of different sensilla on the distal tarsomeres of the forelegs can be



expected. Some authors identified different types of setae and other surface structures on the tarsi and expected them to be sensilla (e.g., Hansen & Sørensen 1904; Pittard & Mitchell 1972; Dumitresco & Juvara-Bals 1973, 1976; Legg 1976), but information about their ultrastructure and possible function are still not available. In the present work, we intend to present the first ultrastructural study of the pore organ of the foreleg tarsi of Ricinulei.

## METHODS

The distal tarsomeres of leg I and II of two cavernicolous Mexican species were examined in this study. Specimens of *Pseudocellus pearsei* (Chamberlin & Ivie 1938) from Yucatan peninsula were collected in three different caves, Gruta Actún Chen (Quintana Roo; 20° 20' 13" N & 87° 20' 45" W), Gruta X-Caret (Quintana Roo; 20° 33' 54" N & 86° 58' 49" W) and Gruta Sabac-Ha (Yucatán; 20° 10' 18" N & 89° 16' 03" W). *Pseudocellus boneti* (Bolívar and Pieltain 1941) from Guerrero was collected in the caves Grutas de Acuitlapán (Mexico; 18° 38' 00" N & 99° 31' 55" W). Both species have been found in bat guano or under flat stones. For SEM, 7 specimens of *P. pearsei* (1 larva, 1 protonymph, 1 deutonymph, 3 adult males and 1 adult female) and 4 specimens of *P. boneti* (1 larva, 1 tritonymph and 2 adult males) stored in ethanol (70%) were dehydrated in graded ethanols, critical-point dried and coated with gold-palladium. Examination was performed on a LEO DSM 940. For TEM the distal tarsomeres I and II of 5 specimens of *P. pearsei* (3 deutonymphs and 2 adult males) were dissected in ice-cold Sørensen phosphate buffer (pH 7.4; 0.1 M) and then fixed in 3.5% glutaraldehyde buffered in Sørensen phosphate buffer overnight. Further processes included postfixation with OsO<sub>4</sub> (2%) for two hours, rinsing in buffer, dehydration in graded ethanols and embedding mainly in Spurr's medium (Spurr 1969) and alternatively in Epon-Araldite. Ultrathin sectioning with a Diatome diamond knife took place on a Leica Ultracut. Sections were stained with saturated uranylacetate (in 70% methanol) for 5 minutes and lead citrate according to Reynolds (1963) for 15 minutes. The sections were examined with a Zeiss EM 10 A. For general orientation semithin sections (400–700 nm) were used which were stained according to Richardson et al.

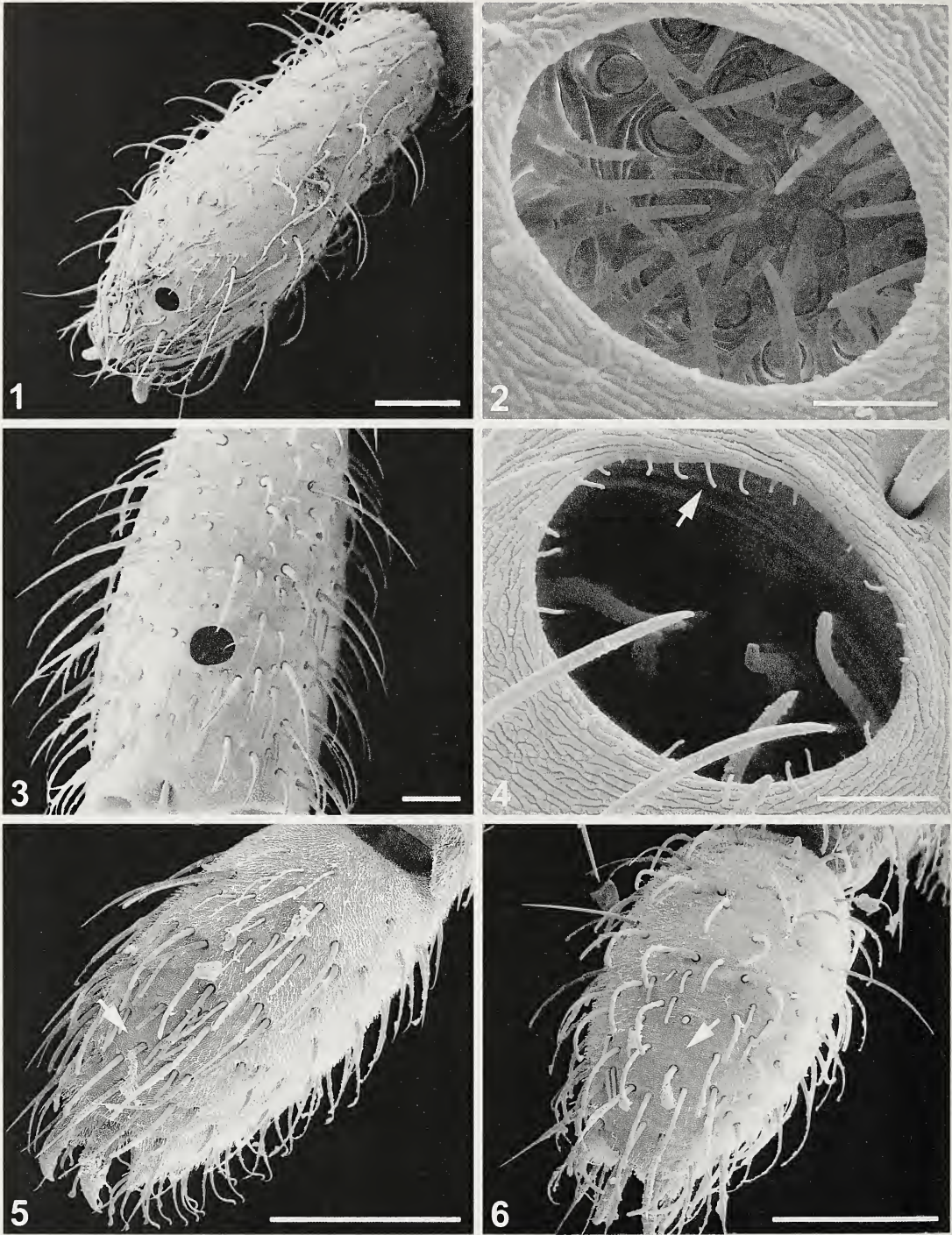
(1960). All sections and voucher specimens are housed in the Zoological Institute & Museum of the University of Greifswald.

## RESULTS

The pore organ is located in the distal third of the dorsal half of the distal tarsomeres of legs I and II (Figs. 1, 3). The width of the opening is about 32 µm in *P. pearsei* and 36 µm in *P. boneti* (Figs. 2, 4). The edge of the opening differs slightly in both species. In *P. pearsei* the edge is smooth without any projections (Fig. 2), while in *P. boneti* there are some short and thin microtrichae which project radially into the center of the opening (Fig. 4). Except for the larvae (Figs. 5, 6), this structure is present on the forelegs of each investigated life stage and both sexes of *P. pearsei* and *P. boneti*. The pore organ extends as a deep tube-like pit into the tarsus. In longitudinal sections it shows a long oval shape (Figs. 7–10). In cross sections it is nearly circular (Figs. 11, 12). Sexual dimorphism could not be observed in the present material.

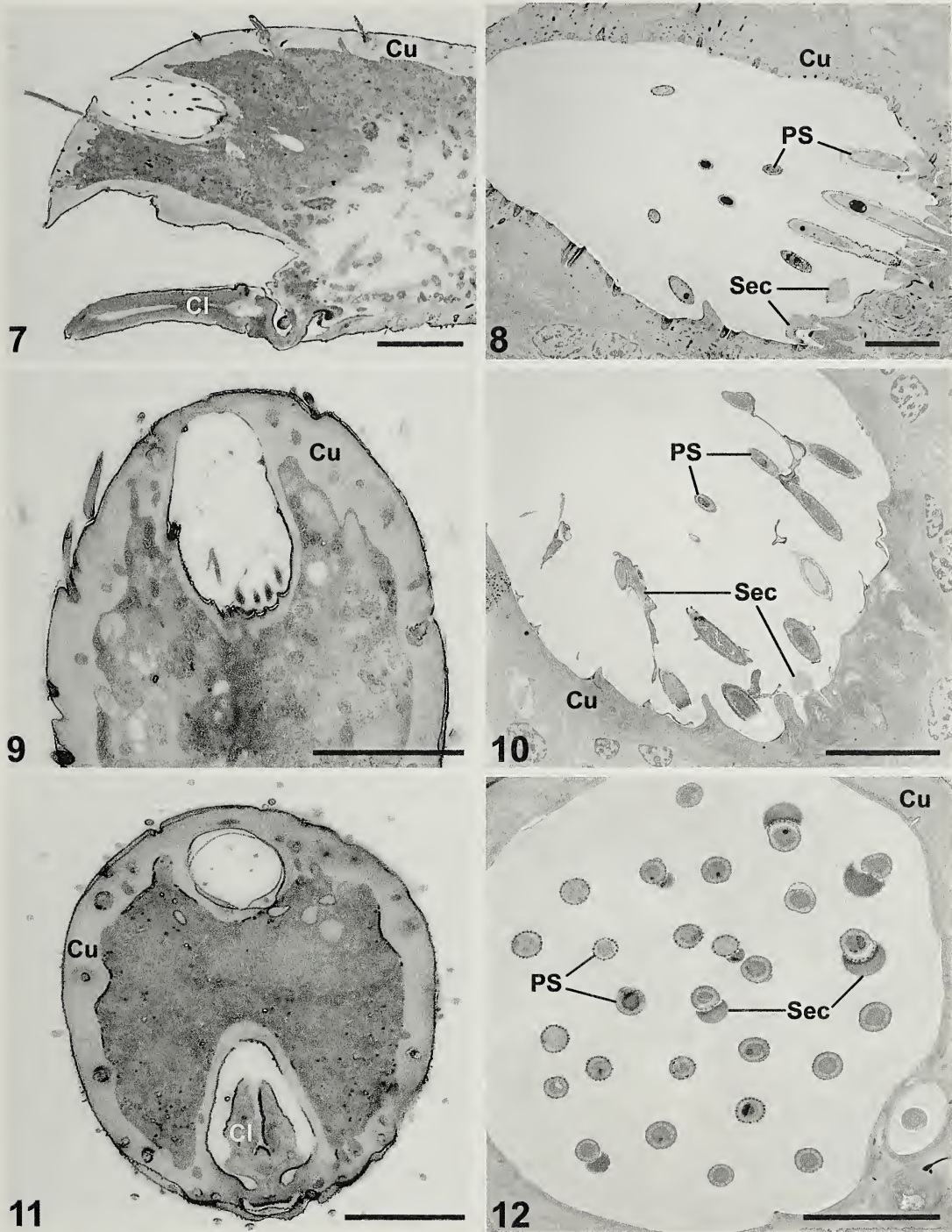
In both species the pore organ contains a large number of long slightly curved setae. These setae are localized on the bottom and the lower two thirds of the wall of the pore organ and project into the lumen but do not reach the opening (Figs. 2, 4, 13). The upper third of the wall is free of setae and shows folds which extend parallel to the opening (Fig. 13, 14). Some small openings in the wall are visible (Fig. 13, 14). In SEM micrographs, the setae show a great number of wall pores (Fig. 15) but in some parts of the shaft the openings of these pores are covered by droplets of different size (Figs. 16, 17). In *P. pearsei* all setae inside the pore organ seem to be of the same type (Fig. 12). Sections reveal the complex wall of these setae. It consists of two layers: a thick inner wall with up to 25 pores per section and a thin outer wall with a similar number of pores which are plugged by electron dense bodies (Figs. 18–20). Some setae are partly surrounded by secretions (Figs. 19). This is very evident in the basal part of the pore organ where most of them arise (Figs. 23, 26). The sockets of the setae are inflexible (Fig. 26). The setae are innervated by 4–7 outer dendritic segments (Figs. 21, 22). These are surrounded by an enveloping cell and many densely arranged microvilli (Fig. 21). The latter are formed by the tormogen cell which





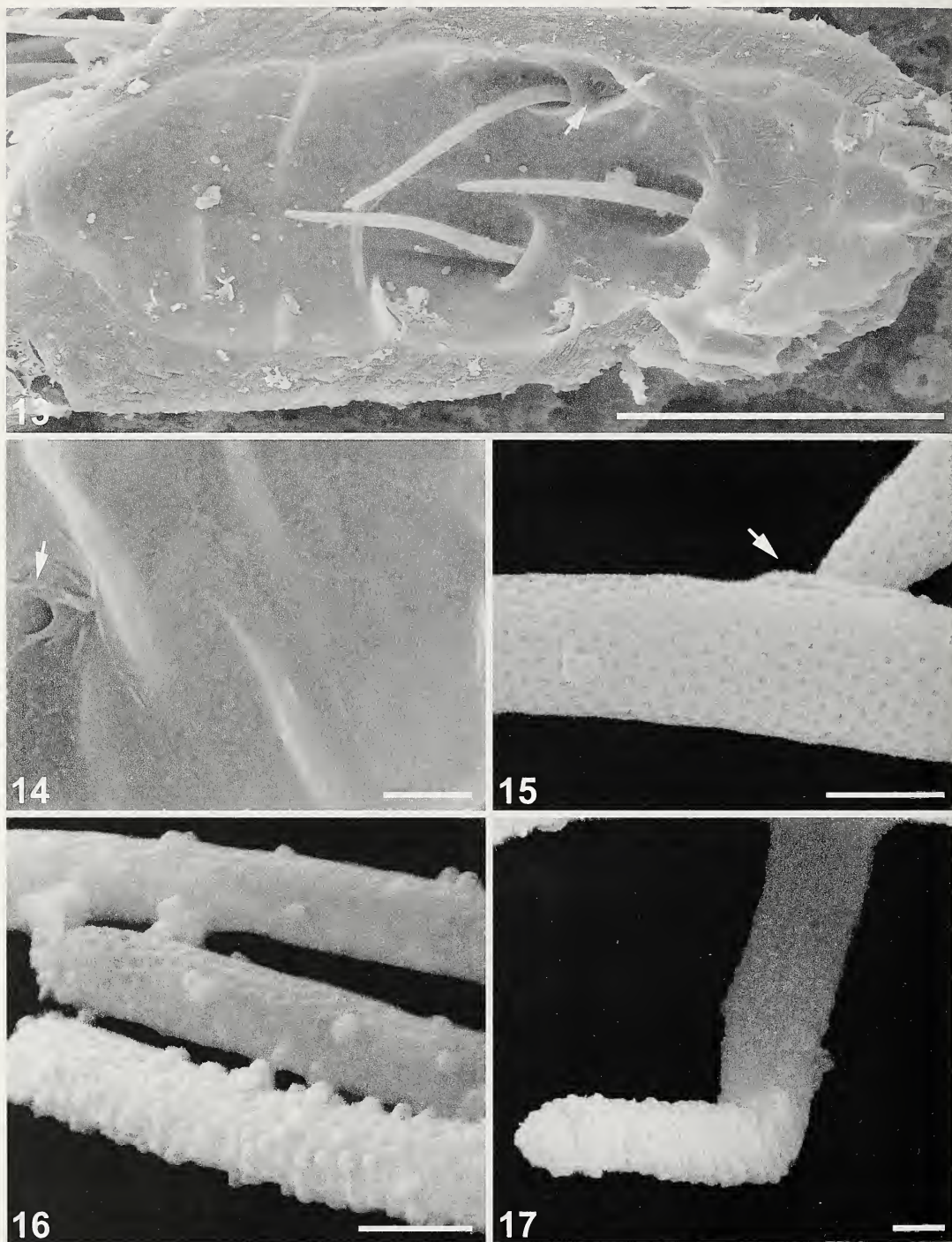
Figures 1–6.—Distal tarsomeres. 1. Tarsus II of *Pseudocellus pearsei* (adult male). Scale bar = 100  $\mu\text{m}$ . 2. Pore organ opening of that tarsus. Scale bar = 10  $\mu\text{m}$ . 3. Tarsus I of *Pseudocellus boneti* (adult male). Scale bar = 50  $\mu\text{m}$ . 4. Opening of the pore organ of tarsus I of *P. boneti* (tritonymph). Note the small microtrichiae (arrow). Scale bar = 10  $\mu\text{m}$ . 5. Tarsus I of *P. pearsei* (larva). Scale bar = 100  $\mu\text{m}$ . 6. Tarsus II of *P. pearsei* (larva). Scale bar = 100  $\mu\text{m}$ . Note the dorsofrontal region of the tarsi without pore organ (arrows).





Figures 7–12.—Light and TEM micrographs of the pore organ of *Pseudocellus pearsei*. 7. Sagittal section of tarsus II. Scale bar = 50  $\mu\text{m}$ . 8. Detail of pore organ with longitudinal and oblique sections of sensilla. Scale bar = 10  $\mu\text{m}$ . 9. Horizontal section of tarsus I. Scale bar = 50  $\mu\text{m}$ . 10. Detail of the pore organ base and some oblique sections of sensilla. Scale bar = 10  $\mu\text{m}$ . 11. Transversal section of tarsus I. Scale bar = 50  $\mu\text{m}$ . 12. Detail of the lumen with cross sections of sensilla. Scale bar = 10  $\mu\text{m}$ . Abbreviations: Cl = claw, Cu = cuticle, PS = pore organ-sensilla, Sec = secretion.





Figures 13–17.—Surface of the pore organ integument and the pore organ-sensilla. 13. Longitudinal section of the pore organ of tarsus I of *Pseudocellus pearsei* (adult female) with three lateral inserted sensilla and a gland opening (arrow). Scale bar = 30  $\mu\text{m}$ . 14. Detail of the integument with folds and a gland opening (arrow). Scale bar = 3  $\mu\text{m}$ . 15. The sensilla shaft of *P. pearsei* with many wall pores. Note the damaged area (arrow). Scale bar = 1  $\mu\text{m}$ . 16. Some sensilla with numerous droplets covering the wall pores. Scale bar = 1  $\mu\text{m}$ . 17. Pore organ-sensillum of *Pseudocellus boneti* with a totally covered surface. Scale bar = 1  $\mu\text{m}$ .



produces the slightly electron dense receptor lymph (Figs. 21, 26). A dendritic sheath is lacking. The dendritic segments terminate in the basal part of the shaft. Pore tubules beneath the wall pores are lacking. The apical part of the shaft is completely filled with receptor lymph of different electron densities (Fig. 18).

Large gland cells which are formed by modified epidermal cells occur between the sensilla forming cells (Figs. 23, 26). The glands appear sack-like and each one forms a large secretion reservoir which is filled with an almost electron lucent material (Figs. 23, 26). Large nuclei, numerous mitochondria, secretion vesicles and microvilli, which project into the reservoirs, are present in these cells (Figs. 23, 26). The secretion seems to be delivered through at least 1 pore, partly filled with granular material, into the lumen of the tarsal pore organ (Figs. 24, 25) but it can not be excluded that a gland cell exhibits more than 1 pore.

#### DISCUSSION

The first short description of the tarsal pore organ was given by Pittard & Mitchell (1972). They named it "deep pit" and found that this structure is not present in the larva but on the distal tarsomeres of leg I and II of all further life stages. Our observations confirm these results for *P. pearsei* and partly for *P. boneti*. Dumitresco & Juvara-Bals (1973) suggested the "organe tarsal" may be comparable to the tarsal organs of other Arachnida. These are present in Araneae, the tarsal organs on palps and walking legs (e.g., Blumenthal 1935; Foelix & Chu-Wang 1973), Scorpiones (Foelix & Schabronath 1983), Amblypygi (Foelix et al. 1975) and in Anactinotrichida, the well known Haller's Organ on tarsus I of Ixodida and Holothyrida and the telotarsal organ on tarsus I of Opilioacarida (summarized by Alberti & Coons 1999; Coons & Alberti 1999). The tarsal organs of the mentioned groups possess several types of sensilla. Olfactory, thermo/hygrosensitive and mechanosensitive receptors could be identified in numerous studies.

The tarsal pore organ of ricinuleids shows similarities to the proximal part of Haller's organ, the capsule, in Ixodida. These capsules bear 2–7 sunken sensilla (see Foelix & Axtell 1972; Coons & Alberti 1999) which have olfactory function. According to the concepts of

pore structures and the function of arthropod sensilla (e.g., Altner 1977; Altner & Prillinger 1980; Tichy & Barth 1992; Steinbrecht 1997; Hallberg & Hansson 1999), three main types of olfactory sensilla are known: 1) single-walled sensilla with simple wallpores, 2) single-walled sensilla with plugged wallpores and 3) double-walled sensilla with spoke canals. Single-walled sensilla with plugged wallpores are present in the capsule of Haller's organ (Foelix & Axtell 1972). The wall of the pore organ-setae of *P. pearsei* differs in structural details from the main types described above and also from the capsule-sensilla of Ixodida. Although wall pores with some kind of pore plugs are clearly present, the complex thin outer layer (Figs. 18–20), which may consist of another type of secretion instead of cuticle, makes it difficult to assign the pit-setae to one type of sensilla. Foelix & Axtell (1972) described a thin layer of "extracellular material" which often covers the capsule-sensilla, but this layer has no complex structure. It is not clear whether this layer consists of receptor lymph or other secretions but the authors note that it was only prominent after simultaneous glutaraldehyde-OsO<sub>4</sub> fixation which was not performed in this study. Indeed the phenomenon of droplets appearing on the surface of sensilla (Figs. 16, 17) is explained as dried receptor lymph (Foelix & Schabronath 1983). Altner (1977) pointed out that pore structures exist which do not fit to the classification system of sensilla types. However, the presence of wall pores and innervating dendrites (Figs. 15–22) in the pore organ-setae of *P. pearsei* indicate an olfactory function. The limited material does not allow the reconstruction of the exact innervation pattern (e.g. number and organization of neurons) of this organ. Therefore further investigations are needed. According to Foelix & Axtell (1972) and with regard to the more or less endogenous living of ricinuleids we believe that the tarsal pore organ serves, similar to the capsule of Haller's organ of Ixodida, mainly as a protective device for numerous olfactory sensilla, which could easily be damaged mechanically if been exposed to the tarsal surface. However, only electrophysical proofs can verify the sensory function of an organ (see e.g., Dumpert 1978; De Bruyne & Guerin 1994).

In Ixodida a large multicellular gland beneath the capsule is known (Foelix & Axtell





Figures 18–26.—Ultrastructure of the tarsal pore organ of *Pseudocellus pearsei*. 18. Cross section of a pore organ-sensillum (apical shaft). Scale bar = 0.5  $\mu$ m. 19. Cross section of the basal shaft with droplets of secretion. Scale bar = 0.5  $\mu$ m. 20. Detail of the wall. Scale bar = 0.2  $\mu$ m. 21. Transverse section of a sensillum socket with 4 outer dendritic segments (inset). Scale bars = 0.5  $\mu$ m, 0.2  $\mu$ m. 22. Horizontal section of dendrites beneath a sensillum. Scale bar = 1  $\mu$ m. 23. Horizontal section of the pore organ base with gland cells between the sensilla forming cells (asterisks). Scale bar = 5  $\mu$ m. 24. Transverse section of pores (arrows) in the integument between sensillum sockets. Scale bar = 0.5  $\mu$ m. 25. Horizontal section of a pore filled with granular material (arrow). Scale bar = 0.5  $\mu$ m. 26. Detail of Fig. 23. Scale bar = 2  $\mu$ m. Abbreviations: Cu = cuticle, eC = enveloping cell, gR = glandular reservoir, iL = inner layer, Mi = mitochondria, Mv = microvilli, N = nucleus, oD = outer dendritic segment, oL = outer layer, PP = pore plug, RLy = receptor lymph, Sec = secretion, tC = tormogen cell.



1972). Their glandular openings were found in the capsule wall. It was suggested that this gland might be the origin of the material surrounding the capsule-sensilla. The large glands beneath the pore organ of *P. pearsei* are supposed to produce the secretion present between the sensilla and on their surface (Figs. 19, 23–26). They are believed to represent enlarged unicellular “class I” epidermal glands according to the classification of Noirot & Quennedy (1974, 1991). Such glands pour their secretions through a simple pore without any special canal formation (Figs. 13, 14, 24, 25). The secretion may support the binding of odorants or probably rinses the sensilla surfaces to keep them clean.

However, some main differences between Haller's organ of Ixodida and the tarsal organ of ricinuleids are evident. The tarsal pore organ of ricinuleids occurs on leg I and leg II not only on leg I like in ticks and it contains many more sensilla than the capsule of ticks. Furthermore Haller's organ is present in ixodid larvae but the tarsal pore organ is not present in the larva of ricinuleids. In ticks Haller's organ is the main receptor for host detection in all life stages (Foelix 1985). Ricinuleids are not parasitic. If olfactory function can be confirmed in the future, detection of other odorants can be expected. Like in Araneae (DumPERT 1978) pheromone detection is imaginable, because this might not be important for the larvae. Unfortunately, the knowledge of the biology of these animals, in particular the dynamics between individuals in their habitats is still too poor to enable any suggestions in this case. For these reasons, further investigations including also species of the other two genera and on the biology of Ricinulei are required.

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# ULTRASTRUCTURE OF MALE GENITAL SYSTEM AND SPERMATOOZOA OF A MEXICAN CAMEL-SPIDER OF THE *EREMOBATES PALLIPES* SPECIES GROUP (ARACHNIDA, SOLIFUGAE)

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**ABSTRACT.** The male genital system of Solifugae is divided into three different parts: a) a common genital chamber, b) the paired tubular vasa deferentia and c) the long, thin testes. On each side, the vas deferens splits into two smaller branches resulting in the thin, extremely long testes such that one individual possesses four tubular testes in total. The epithelium of a testis consists mainly of a glandular part and of a germinal part surrounded by a small layer of muscles. In *Eremobates* sp., within the germinal part the sperm cells are groups of a few, probably four, mature sperm cells each surrounded by thin extensions of somatic cells. These somatic cells can clearly be distinguished from the cells forming the glandular part which contain large amounts of rough endoplasmic reticulum. Once released into the narrow testicular lumen, the spermatozoa float more or less individually in a proteinaceous secretion. Earlier stages of spermatogenesis could not be detected, suggesting that spermatogenesis may occur in the subadult male (not examined in this study). In general, the sperm is rather simple, representing a round or slightly elongated cell devoid of a flagellum. The relatively small and flat acrosomal vacuole is attached to the disc-like nucleus. The acrosomal filament penetrates the nucleus and is coiled several times around it. In contrast to species of the family Ammotrechidae or Karschiidae, for which sperm cells have already been described, the sperm cells of the Mexican *Eremobates* sp., which belongs to the family Eremobatidae, show no tendency to form any piles or well ordered groups in the lumen of either the testes or the vasa deferentia.

**Keywords:** Solifugae, genital system, sperm cell, systematics

Most camel-spiders (Arachnida, Solifugae), also called sunspiders or wind-scorpions, inhabit tropical, subtropical regions and arid environments in southern Europe, Africa, Asia and the Americas (Punzo 1998). The oldest specimen of Solifugae is known from the Upper Carboniferous (Pennsylvanian in US terminology) of Mazon Creek, Illinois, USA (Selden & Shear 1996). Most of the 1084 recent species (Harvey 2002) are nocturnal predators known for their extreme rapidity. The huge chelicerae represent a characteristic feature of their external morphology and they can be easily distinguished from other arachnids by the presence of racquet organs (mallooli). Their position within the Arachnida is not yet fully resolved, since Solifugae express both apomorphic (e. g. highly developed tra-

cheal system, two-jointed chelicerae) and plesiomorphic (e. g. segmentation of the opisthosoma) characteristics (Roewer 1934; Moritz 1993), but they are usually considered to be the sister-group of the Pseudoscorpiones (Weygoldt & Paulus 1979; Shultz 1990; Weygoldt 1998; Wheeler & Hayashi 1998; Dunlop 2000; Giribet et al. 2002). In any case, Roewers classification of the order Solifugae is based on a small set of character systems and therefore lacks a reliable basis for phylogenetic and subsequent systematic implications (Harvey 2002).

So far, only a few electron microscopic studies on this animal group have been completed (see e.g., Brownell & Farley 1974; Alberti 1979, 1980; Bauchhenss 1983; Ludwig & Alberti 1992; Alberti & Peretti 2002). Ac-

cording to the current literature, the ventrally located male genital system of Solifugae is generally divided into three different parts: a) a common genital chamber, b) the paired tubular vasa deferentia and c) the long, thin testes. Even though there are several studies on this organ system (see e.g. Roewer 1934; Warren 1939; Junqua 1966), the nomenclature concerning the different parts of the genital system varies considerably between these authors. Only the testes and partly the vasa deferentia have been fine-structurally investigated (Alberti 1980; Alberti & Peretti 2002). The aim of the present study was to confirm and to substantiate the present knowledge on the male reproductive system and sperm morphology and to present the first ultrastructural study of the genital chamber and its accessory glands.

## METHODS

Males of the genus *Eremobates* Banks 1900, belonging to the *Eremobates pallipes* (Say 1823) species group according to Brookhart (pers. comm.), were captured near Pachuca-City, State of Hidalgo, Mexico (20°07'21"N, 98°44'09"W). After dissection of three males in ice-cold cacodylate buffer their genital systems were fixed in 3.5 % glutaraldehyde buffered in cacodylate buffer (pH 7.4; 0.1 M). Fixed genital systems were sent to Germany in diluted glutaraldehyde. Postfixation processes included treatment with OsO<sub>4</sub> (2 %) for two hours, rinsing in buffer solutions, dehydration in graded ethanols (60–100 %) and embedding in Spurr's medium (Spurr 1969). Ultrathin sections of approximately 70 nm were cut with a Diatome diamond knife using a Leica Ultracut microtome. Sections were stained with saturated uranylacetate (in 70 % methanol) and lead citrate according to Reynolds (1963). For general orientation semithin sections (700 nm) were used which were stained according to the methods of Richardson et al. (1960). Transmission electron microscopy was performed using a Zeiss EM 10 A transmission electron microscope. For scanning electron microscopy, the genital system was dehydrated in graded ethanols (60–100 %), then coated with gold-palladium and finally investigated with a LEO DSM 940. A male *Eremobates* sp. has been deposited as a voucher specimen in the Museo Argentino de

Ciencias Naturales "Bernardino Rivadavia" (MACN) in Buenos Aires.

## RESULTS

**Scanning electron microscopical observations.**—In general, the male genital system consists of a common genital chamber, the vasa deferentia and the testes. Immediately after being removed from the male, the fresh genital system is translucent yellow. The paired tubular vasa deferentia originate from the genital chamber to which small accessory glands are directly attached. Each vas deferens splits into two smaller branches each resulting in extremely long, thin testes which are only partly shown in Fig. 1.

**Light and transmission electron microscopical observations.**—*Testes:* The long, thin tubular testes are surrounded by small muscle cells. The somatic epithelium is composed of a larger glandular and a comparatively small part in which the germinal cells are embedded (so called germinal part). Cells of the glandular part are characterized by many cisternae of rough endoplasmic reticulum and Golgi bodies, often located close to the nucleus. Their nuclei are more or less rounded or slightly oval in shape, approximately twice as large as the nuclei of the somatic cells of the germinal part and located in the basal half of the cells (Fig. 2). Branching somatic cells forming a meshwork constitute the germinal part in which groups of sperm cells are embedded (Fig. 3). In contrast to the cells of the glandular part, the somatic cells of the germinal part are irregularly shaped and contain only a few cell organelles. Apically, in both somatic cell types there is a border of microvilli. Each sperm group consists of a few, probably four, mature sperm cells (Fig. 3). No spermatogenesis could be observed. The sperm cells float more or less distinctively in the narrow testicular lumen containing different kinds of proteinaceous secretions most likely produced by the glandular cells (Fig. 4). Towards the vasa deferentia and shortly before the testes open into the vas deferens, the epithelium flattens and no spermatozoa can be observed in the tissue. The sperm cells are rather simple, representing a roundish or slightly elongated cell body devoid of a flagellum, but provided with one, rarely two, flat extensions which fold onto the cell body (Fig. 8, 9, 10). In general, the following character-



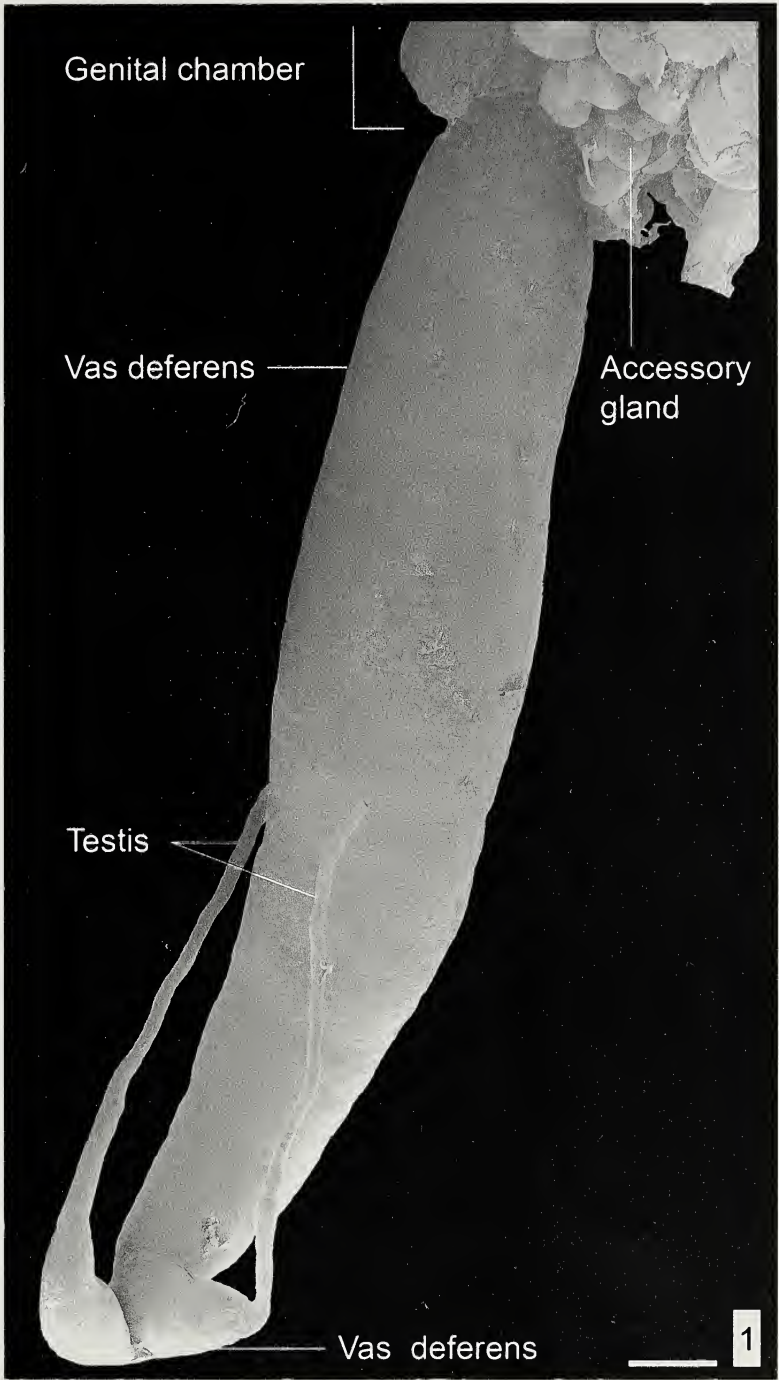
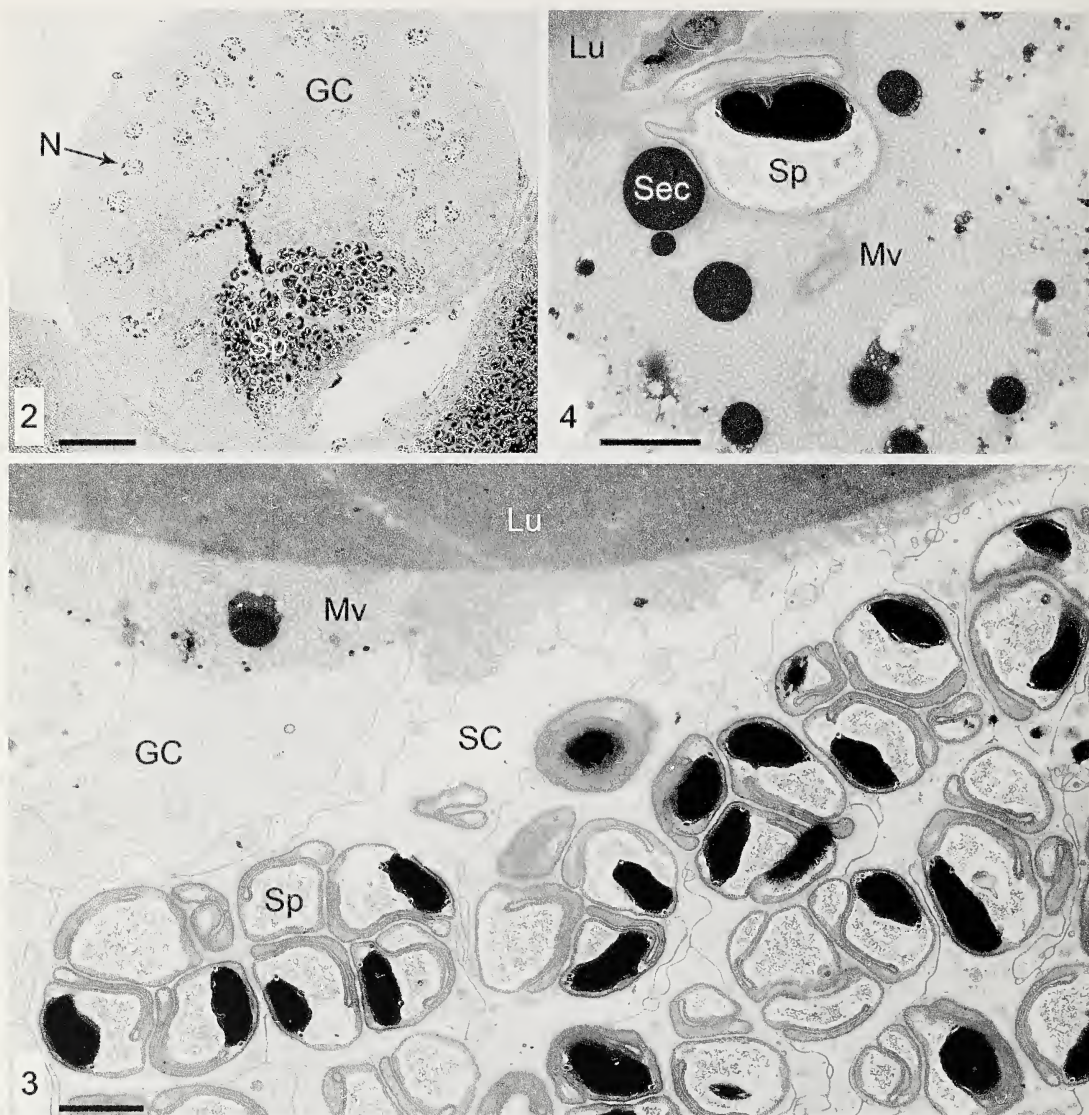


Figure 1.—Scanning electron micrograph of the left side of the male genital system of *Eremobates* sp. (genital chamber and testes are only partly shown; composed picture). Scale bar = 300  $\mu$ m.

istic cell components can be distinguished in the mature spermatozoa: acrosomal complex, nucleus and cytoplasm including a more or less electron-lucent area. The acrosomal com-

plex can be divided into an acrosomal vacuole, amorphous subacrosomal material and the acrosomal filament (perforatorium) starting from the amorphous subacrosomal material.

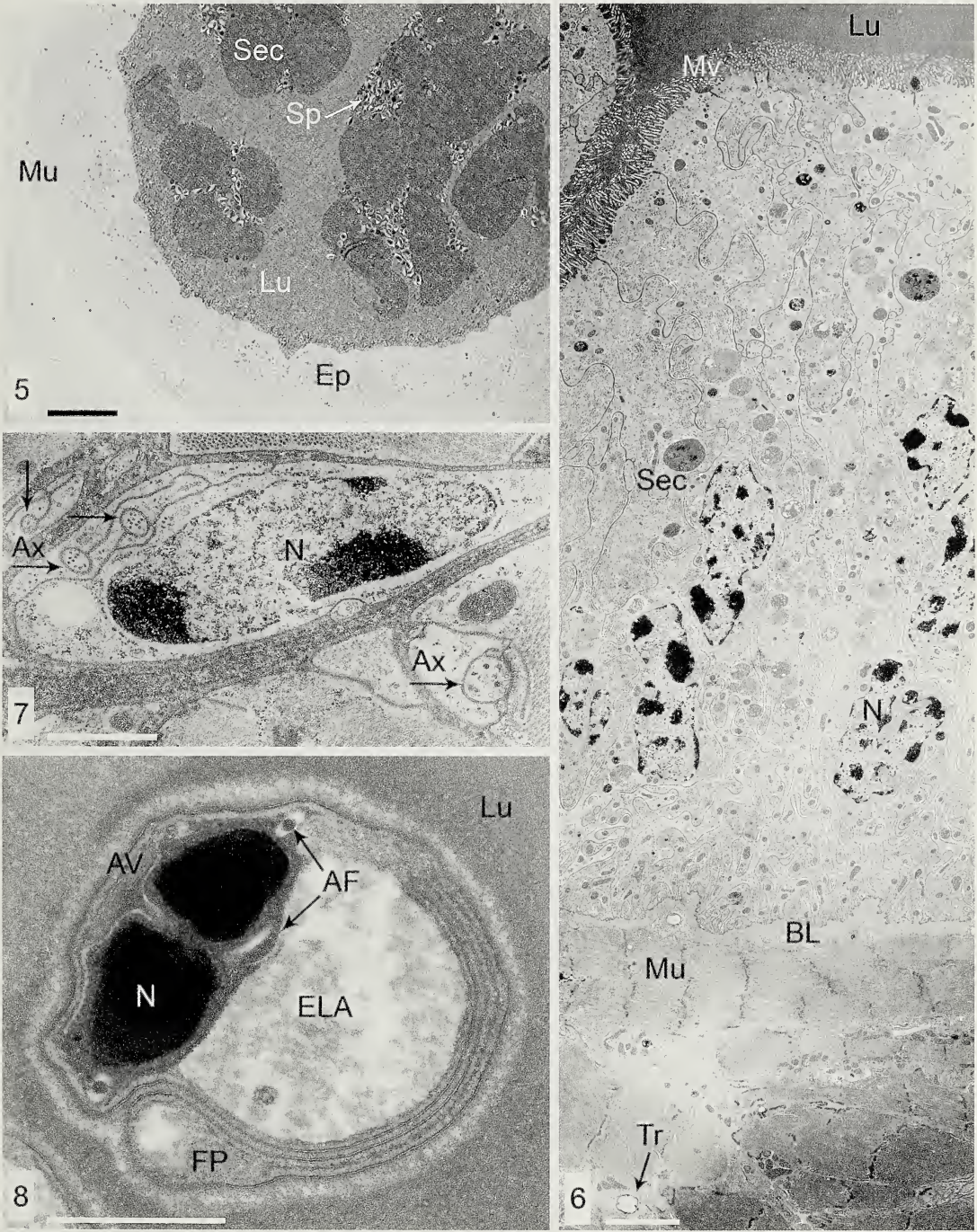


Figures 2–4.—Testis. 2. Light micrograph of the transversal section through the testis showing germinal and glandular part. Scale bar = 50  $\mu\text{m}$ . 3. Groups of four spermatozoa embedded in somatic cells of the germinal layer. Left, glandular cells. Scale bar = 2  $\mu\text{m}$ . 4. Sperm cell in the lumen of the testis surrounded by globules of secretions. Scale bar = 2  $\mu\text{m}$ . Abbreviations: GC = glandular cell, Lu = lumen of the testis, Mv = microvilli, N = nucleus, SC = somatic cell, Sec = secretion, Sp = sperm cell.

The relatively small acrosomal vacuole is attached to the electron-dense nucleus. The nucleus is penetrated and surrounded by the acrosomal filament (Figs. 8, 9). A conspicuous flat extension of the cell contains no organelles and slightly inflates towards its posterior end. The sperm cells show no tendency to form well ordered piles or globules either in the lumina of the testes or in the vasa deferentia.

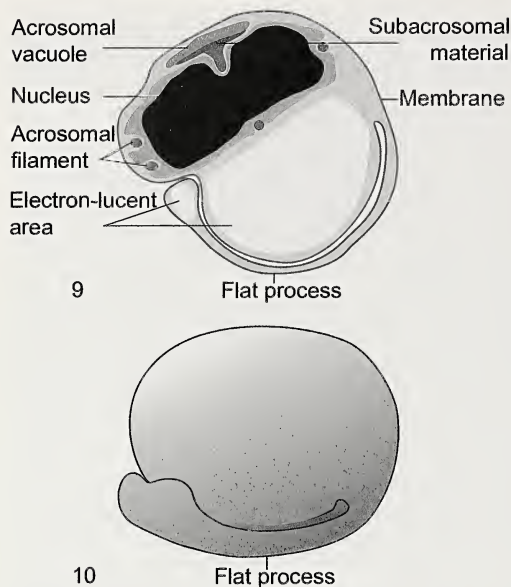
*Vas deferens:* The epithelium of the vas deferens is underlain by a relatively thick outer cross-striated muscle layer interlaced with small tracheae (Figs. 5, 6). The epithelial cells are connected to the basal lamina via hemidesmosomes. The nuclei of the cells of the epithelium, containing considerable amounts of rough endoplasmic reticulum, are irregularly shaped. The wide lumen is filled with different kinds of secretions forming distinct





Figures 5-8.—Vas deferens. 5. Light micrograph of the small branch of the vas deferens. Scale bar = 50  $\mu$ m. 6. Epithelium of the smaller branch of the vas deferens underlain by a muscle layer (composed picture). Scale bar = 4  $\mu$ m. 7. Nerve fibres (indicated by arrows) within the muscle layer. Scale bar = 1  $\mu$ m. 8. Single sperm cell in the lumen of the vas deferens. Scale bar = 1  $\mu$ m. Abbreviations: AF = acrosomal filament, AV = acrosomal vacuole, Ax = axon, BL = basal lamina, ELA = electron-lucent area, Ep = epithelium, FP = flat process, Lu = lumen of the vas deferens, Mu = muscle, Mv = microvilli, N = nucleus, Sec = secretion, Sp = sperm cells, Tr = trachea.





Figures 9, 10.—Schematic drawings of a sperm cell. 9. Longitudinal section. 10. Three-dimensional reconstruction of the sperm body.

globules and mature sperm cells (Fig. 5). The muscle layer is innervated as indicated by the number of nerve fibres observed between the cells (Fig. 7).

**Genital chamber:** Several glandular pouches extend from the genital chamber and constitute the accessory glands. The glands are provided with an epithelium characterized by many rough endoplasmic cisternae, which are often inflated (Fig. 11). Secretory vesicles are only rarely observable. Apically, the cells bear microvilli (Fig. 12). The epithelium is underlain by thin muscle cells.

The genital chamber is directly connected to the genital opening located on the second opisthosomal segment. In certain regions the epithelium forms many finger-like processes extending into the lumen (Fig. 13). The epithelium of the genital chamber consists of a monolayer of cells which are characterized by basal membrane infoldings associated with mitochondria, thus forming a typical basal labyrinth (Fig. 14). Apically, the epithelium is provided with small microvilli over which a thin cuticle is located (Fig. 15). The cells sometimes contain extensive areas filled with glycogen (Fig. 16). A thick muscle layer, which is innervated, is located under the epithelium.

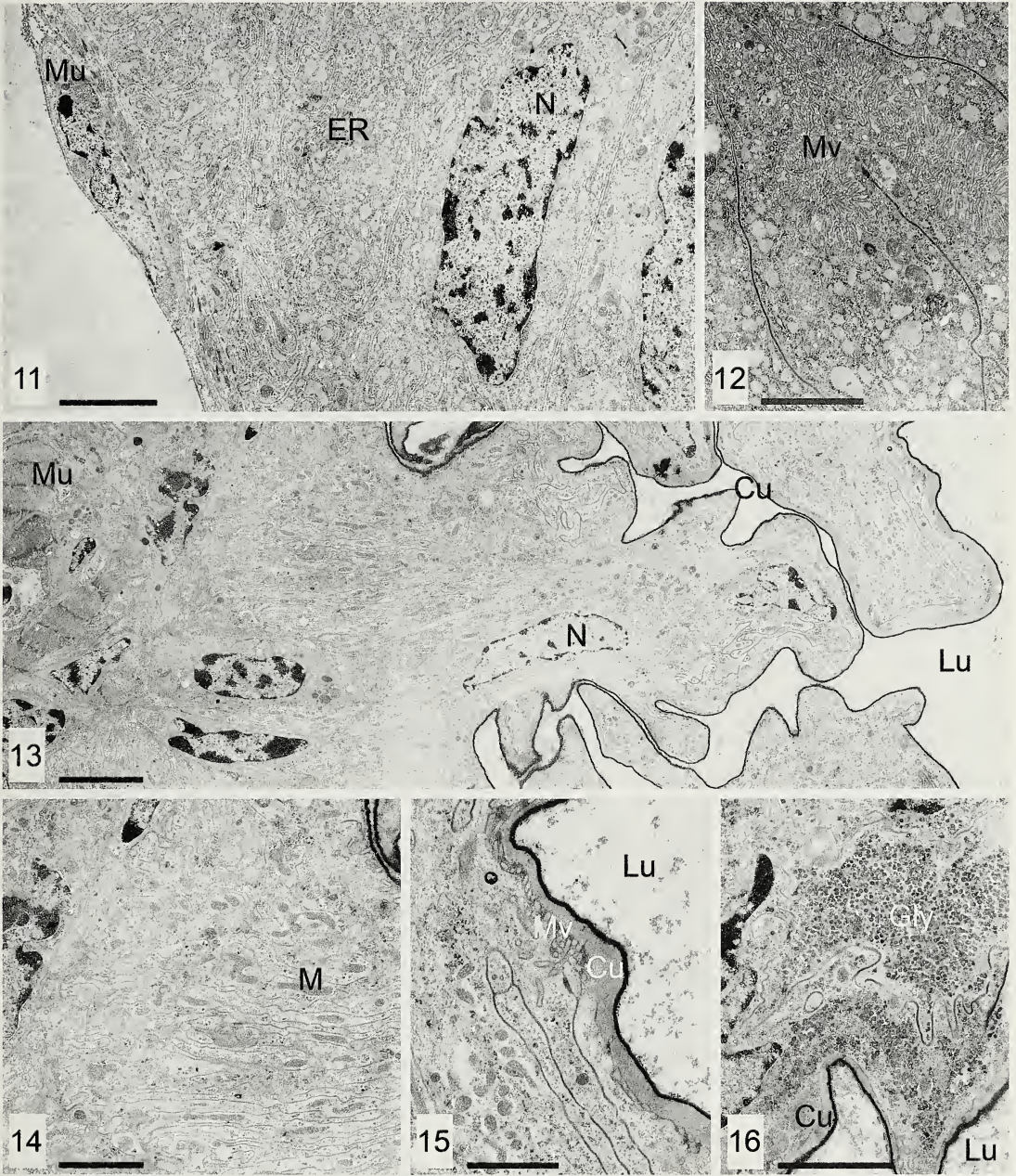
## DISCUSSION

The two functionally different types of the epithelial cells of the testes in Solifugae have already been described by Alberti (1980) and Alberti & Peretti (2002). Our observations concerning the fine structure of the sperm cells agree with earlier results confirming the relatively simple ground pattern of sperm morphology in Solifugae. Nevertheless there are differences in the arrangement of the sperm. The observed spectrum in Solifugae covers highly ordered sperm cells in piles, both in the epithelium of the testes, in its lumen and in the lumen of the vas deferens of a karschiid species, groups of sperm that are less ordered and less compact in an ammotrechid representative and individual cells at least in the lumen of the vas deferens shown in an ammotrechid and the eremobatid species from Mexico studied here. Furthermore the sperm cells differ in shape and structural details. Some types of sperm cells exhibit membrane protuberances to various degrees whereas such structures cannot be observed in other representatives at all. However, it is still too early to apply these results to the systematics of Solifugae, since more species from other families need to be examined. The innervated musculature of the vasa deferentia is certainly involved in the transport of the sperm towards the genital opening and perhaps in releasing the sperm fluid.

Reports on sperm transfer differ. According to Heymons (1902), Cloudsley-Thompson (1961), Amitai et al. (1962) and Peretti & Willemart (unpub. data) sperm fluid is transferred semi-directly. A spermatophore or a sperm droplet is deposited by a male on the ground and subsequently picked up with his chelicerae and transferred to the genital orifice of the female. In contrast, Muma (1966, 1967) and Punzo (1998) reported a direct sperm transfer in the eremobatid solpugids *Eremobates durangonus* Roewer 1934, *E. palpisetulosus* Fichter 1941 and *E. nodularis* Muma 1951 from the genital orifice of a male to that of one of the female.

The function of the accessory glands is speculative. One possibility is that they could take part in the formation of the sperm droplet. The extrusion of the secretion seems not to happen earlier than mating, since the lumina were almost empty in our specimens. A





Figures 11–16.—Genital chamber. 11. Periphery of an accessory gland (composed picture). Scale bar = 3  $\mu$ m. 12. Cell apices of an accessory gland. Scale bar = 2  $\mu$ m. 13. Epithelium overlain by a thin cuticle (composed picture). Scale bar = 5  $\mu$ m. 14. Basal labyrinth characterized by membrane infoldings associated with mitochondria. Scale bar = 3  $\mu$ m. 15. Cell apices of the epithelium with border of small microvilli. Scale bar = 2  $\mu$ m. 16. Glycogen granules. Scale bar = 2  $\mu$ m. Abbreviations: Cu = cuticle, ER = endoplasmic reticulum, Gly = glycogen granules, Lu = lumen, M = mitochondrion, Mu = muscle, Mv = microvilli, N = nucleus.



further source of secretion contributing to the formation of the sperm droplet could be the huge vasa deferentia and the glandular part of the testes. A similar function is known from actinotrichid mites (e.g., Alberti & Coons 1999).

Adults, in particular males, live only a short period of time after mating (Heymons 1902; Punzo 1998). Heymons (1902) in particular emphasized that the spermatophore (i.e. the drop containing sperm fluid) is reduced in size after several copulations. Junqua (1966) proposed that spermatogenesis occurs in subadult males prior to the adult molt which is supported by our ultrastructural investigations of adult males in which spermatogenesis was never detected (see also Alberti 1980; Alberti & Peretti 2002). Therefore it is reasonable to suggest that the testes and the vasa deferentia of an adult male serve only as storage sites for sperm cells until they are transferred during mating.

The apomorphic similarities in sperm cells and in the fundamental organization of the testicular tissue between Solifugae and actinotrichid mites have been pointed out by Alberti (1980) and Alberti & Peretti (2002). Although the Solifugae are commonly regarded as the sister-group of Pseudoscorpiones (together forming the taxon Haplocnemata, e.g. Weygoldt & Paulus 1979; Dunlop 2000), there are tremendous differences in sperm morphology. Pseudoscorpiones possess complex coiled-flagellate spermatozoa (e.g., Werner & Bawa 1988; Dallai & Callaini 1990; Alberti 2000). Thus, comparative spermatology does not support a close relationship between these two animal groups. However, the assumption that the Acari represent a monophylum may be questioned (Alberti 2000; Alberti & Peretti 2002). It may be argued that the differences in the mode of sperm transfer, indirect spermatophore transfer in Pseudoscorpiones and direct or semi-direct in Solifugae, may consequently be reflected in different sperm types. These differences may not necessarily contradict a sister-group relationship between Pseudoscorpiones and Solifugae. However, it can be shown in other arachnid taxa with comparable sperm transfer, e. g., Araneae or Ricinulei, that sperm morphology is not necessarily modified in the same manner as in Solifugae or actinotrichid mites (Alberti 2000). Furthermore, actinotrichid mites show

three kinds of sperm transfer: indirect spermatophore transfer, direct spermatophore transfer using gonopods and direct insemination via a penis, all possessing simple aflagellate spermatozoa. Evidently there is no simple correlation between sperm structure and mode of sperm transfer (Weygoldt 1990, Alberti & Peretti 2002). The similarity in the testis histology in the Solifugae and actinotrichid mites is remarkable. If the Solifugae are closely related to the Pseudoscorpiones (as suggested above), the similarity of the testis histology and the aflagellate sperm must be seen as homoplastic. Another interesting aspect is the occurrence of a transport epithelium in the genital chamber, characterized by conspicuous infoldings of membranes associated with numerous mitochondria. Such a distinct epithelium is also present in the genital papillae of actinotrichid mites (Alberti & Coons 1999), but evaluation of this character in terms of phylogenetic systematics requires further investigations on a broader range of taxa.

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## TERGAL AND SEXUAL ANOMALIES IN BOTHRIURID SCORPIONS (SCORPIONES, BOTHRIURIDAE)

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**ABSTRACT.** New data concerning developmental anomalies observed among species of the family Bothriuridae (Scorpiones) are presented. Tergal malformations in *Bothriurus coriaceus*, *Brachistosternus roigalsinai* and *Bothriurus noa* are described and illustrated. Two new cases of intersexuality in scorpions, in specimens of *Brachistosternus pentheri* and *Bothriurus araguayae*, are reported and discussed.

**Keywords:** Developmental anomalies, tergites, intersexuality, Scorpiones, Bothriuridae

There are numerous reports of developmental anomalies in scorpions (Table 1). Most reports relate to the duplication of posterior body segments (Vachon 1952; Hjelle 1990; Sissom & Shelley 1995, see the latter for overview); reference to other types of developmental anomalies in scorpions is scarce. One work includes information about anomalies of the legs and pedipalps (Armas 1977) and another describes a tergal and two carapacial malformations (Armas 1976). Most recently, Teruel (2004) presented a list and brief description of tergal (see below) and pedipalpal anomalies; however, only Armas (1977) illustrated the anomalies described, a prerequisite for understanding the anomalies reported.

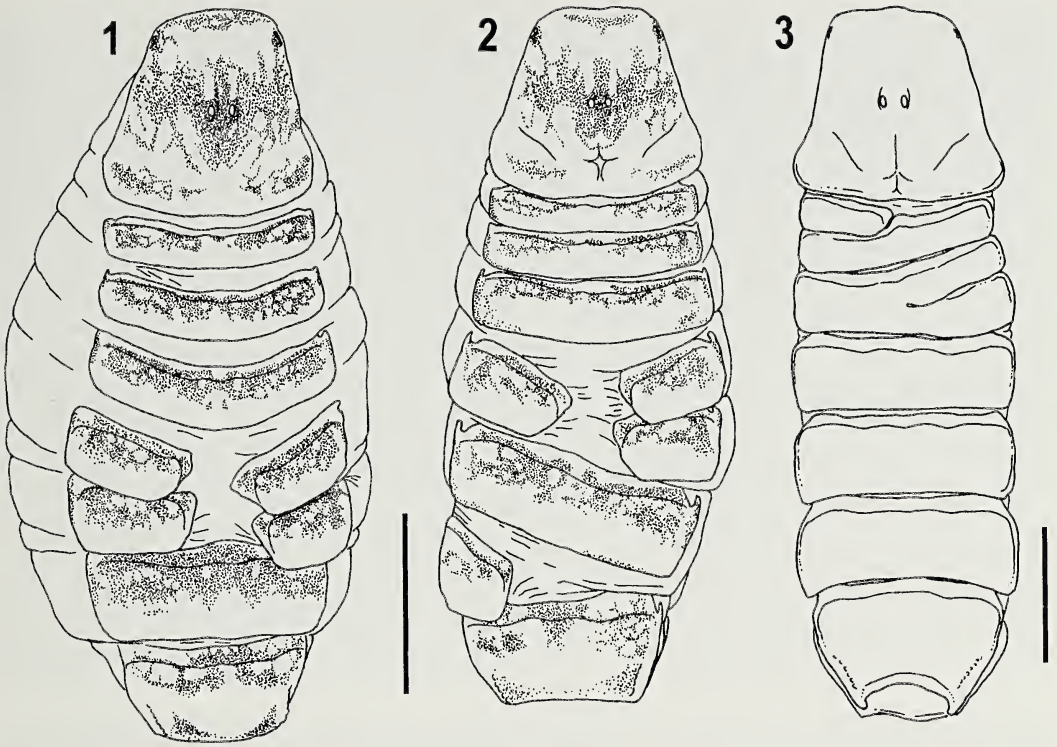
Teruel (2004: 237) references a “chelicerar anomaly” on one specimen of a buthid, *Lychas obsti* Kraepelin 1913. This specimen has two teeth on the ventral surface of the fixed finger of one chelicera and one on the other, the latter expression being the typical condition for *Lychas* (Vachon 1963; Kovařík 1997). Teruel (2004) notes that this is interesting from a taxonomic viewpoint, because, traditionally, the number of ventral teeth on the fixed finger has been used as a strong character in the generic differentiation of the scorpions of the family Buthidae (Kraepelin 1899; Sissom 1990). Teruel (2004) suggested that using this character to identify buthids from Northwest Africa could present problems, because it could cause erroneous identifications. The two states clearly represent normal variation in morphology, and are not anomalous.

Expression of both states in one specimen is clearly an abnormality and the existence of rare abnormalities does not necessitate the need to abandon these character systems. Furthermore, many systematists have observed this kind of variation on the chelicerae of several species, including cases where both chelicerae are different from the usual morphology of the species (Mattoni 2003; Prendini pers. comm.). They would not consider these represent any obstacle for identifying taxa in question, because these occurrences are rare in scorpion populations, and there are many additional characters that can assist with an identification.

The only references to tergal anomalies in scorpions are the works of Armas (1976), who described a specimen of *Didymocentrus trinitarius* Franganillo 1930 (Diplocentridae) with fusion of the carapace and the first tergite, and Teruel (2004) who described anomalies in one male of *Microtityus jaumei* Armas 1974 (Buthidae), that possessed a double anomaly, with tergite V completely divided on the posterior half, and tergite VII fused dorsally to metasomal segment I. Teruel (2004) also reported two female diplocentrids (*Cazierius parvus* Armas 1984 and *C. gundlachii* (Karsch 1880) and one euscorpoid (*Euscorpius flavicaudis* (DeGeer 1778)), possessing totally divided tergites.

The references to sexual malformations are restricted to 5 reports, involving hermaphroditism (with male and female genitalia), gynandromorphism (with both sexes discretely combined) and intersexualism (where the en-





Figures 1–3.—Carapace and tergites of malformed scorpions. 1–2. Females of *Bothriurus coriaceus*; 1. specimen from 4 km N Los Vilos; 2. specimen from Cuesta de Chacabuco. 3. female of *Brachistosternus roigalsinai*, carapace and tergites. Scale = 5 mm.

tire body is intermediate between sexes). Mathiesen (1968) described a hermaphrodite specimen of the buthid *Tityus bahiensis* (Perty 1833). Cokendolpher & Sissom (1988) described two gynandromorphic diplocentrids (a *Cazierius gundlachii* (Karsch 1880) and *Bioculus comondae* Stahnke 1968). Armas (1990) reported a case of one hermaphrodite *Alayotityus juraguaensis* Armas 1973 and a gynandromorphic specimen of *Tityopsis inaequalis* (Armas 1974) (Buthidae). Maury (1983) described an adult hermaphrodite of *Brachistosternus pantheri* Mello-Leitão 1931 (Bothriuridae) showing intersexual and gynandromorphic characteristics, and with both embryos and hemispermaphores. Another interesting malformation was reported in two males of the bothriurid *Bothriurus bonariensis* (C.L. Koch 1842), found mating with females in the field, yet presenting only one hemispermaphore, the right paraxial organ (that produces the hemispermaphore) being absent in both specimens (Peretti 2000). The last two reports, together with the pedipalps anom-

ally reported by Teruel (2004) on *Centromachetes pocockii* (Kraepelin 1894) and *Urophonius granulatus* Pocock 1898, are the only references to malformations among Bothriuridae.

The main goal of this contribution is to describe and illustrate the tergal anomalies that were found in specimens of three Bothriuridae species, and to report two more cases of intersexuality in scorpions.

The specimens studied are preserved in 80 % ethanol and belong to the following collections: AMNH = American Museum of Natural History (New York, USA); MACN-Ar = Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (Buenos Aires, Argentina) and CDA = Cátedra de Diversidad Animal I, Universidad Nacional de Córdoba (Córdoba, Argentina). Illustrations were produced using a Leica MS5 stereomicroscope equipped with a camera lucida. Photographs were taken with an Olympus Stylus 400 digital camera under long-wave ultraviolet light.

**Specimens examined.**—*Bothriurus cori-*

*aceus* Pocock 1893. CHILE: Santiago Region, Chacabuco Province: 1 ♀, Cuesta de Chacabuco, S side, elev. 3900 ft, dry mountainside (32°59' S, 70°44' W), 14 I 1985, N. Platnick, O.F. Francke, AMNH; Coquimbo Region, Choapa Province: 1 ♀, 4 km N Los Vilos (31°72' S, 71°31' W), 5 I 1985, N. Platnick, O. F. Francke, AMNH. *Bothriurus noa* Maury. ARGENTINA: Tucumán Province: 1 ♀ (paratype), Tafi del Valle (26°52' S, 65°51' W), 1970 m, 16 I 1981, E. Maury, MACN-Ar 7571. *Brachistosternus* (*Leptosternus*) *roigalsinai* Ojanguren-Affilastro 2002. CHILE: Atacama Region, Huasco Province: 1 ♀, Llanos de Challe National Park, (28°09'39.8" S, 71°03'20.0" W), 205 m, XII 1997, J. Cepeda-Pizarro, CDA. *Brachistosternus* (*L.*) *pentheri*. ARGENTINA: Mendoza Province: 1 ♂ (?), Reserva de la Biósfera Ñacuñán (34°02' S, 67°54' W), 540 m, 20 XI 2003, C. Mattoni, L. Prendini, J. Ochoa, CDA. *Bothriurus araguayae* Vellard 1934. BRAZIL: Sao Paulo State: 1 ♂ (?), Estação Ecológica de Itirapina, Municipio de Itirapina (22°15' S, 47°49' W), pitfall, 27 VIII 1999, G. Machado.

Two of the females (both *B. coriaceus*) were pregnant when preserved.

**Tergal malformations.**—The *B. coriaceus* specimen from Cuesta de Chacabuco (Fig. 1) shows completely longitudinally divided tergites IV and V. Both parts of each tergite represent almost exactly in shape and size the corresponding half of the tergite; only a small central portion is lacking from the posterior edge. The *B. noa* female shows the same kind of anomaly but only on tergite III.

The specimen of *B. coriaceus* from 4 km N Los Vilos (Fig. 2) also presents some divided tergites, with a different arrangement: tergite IV is completely divided but tergite V is fused sinistrally with the dextral half of tergite VI. The recognition of each part of the tergites is difficult because tergites V and VI are almost the same size.

The *Brachistosternus* (*L.*) *roigalsinai* specimen (Fig. 3) displays a different kind of malformation: the sinistral half of tergite I is free, and the dextral half is joined to the sinistral half of tergite II (one can recognize the tergite because I and II differ in size). The dextral half of tergite II is joined anteriorly to the tergite III.

All observed specimens with tergal anomalies do not show any other evident malfor-

mation, except for the specimen of *B. coriaceus* from Chacabuco that has a slightly abnormal telson vesicle, with the left ventral side a little depressed.

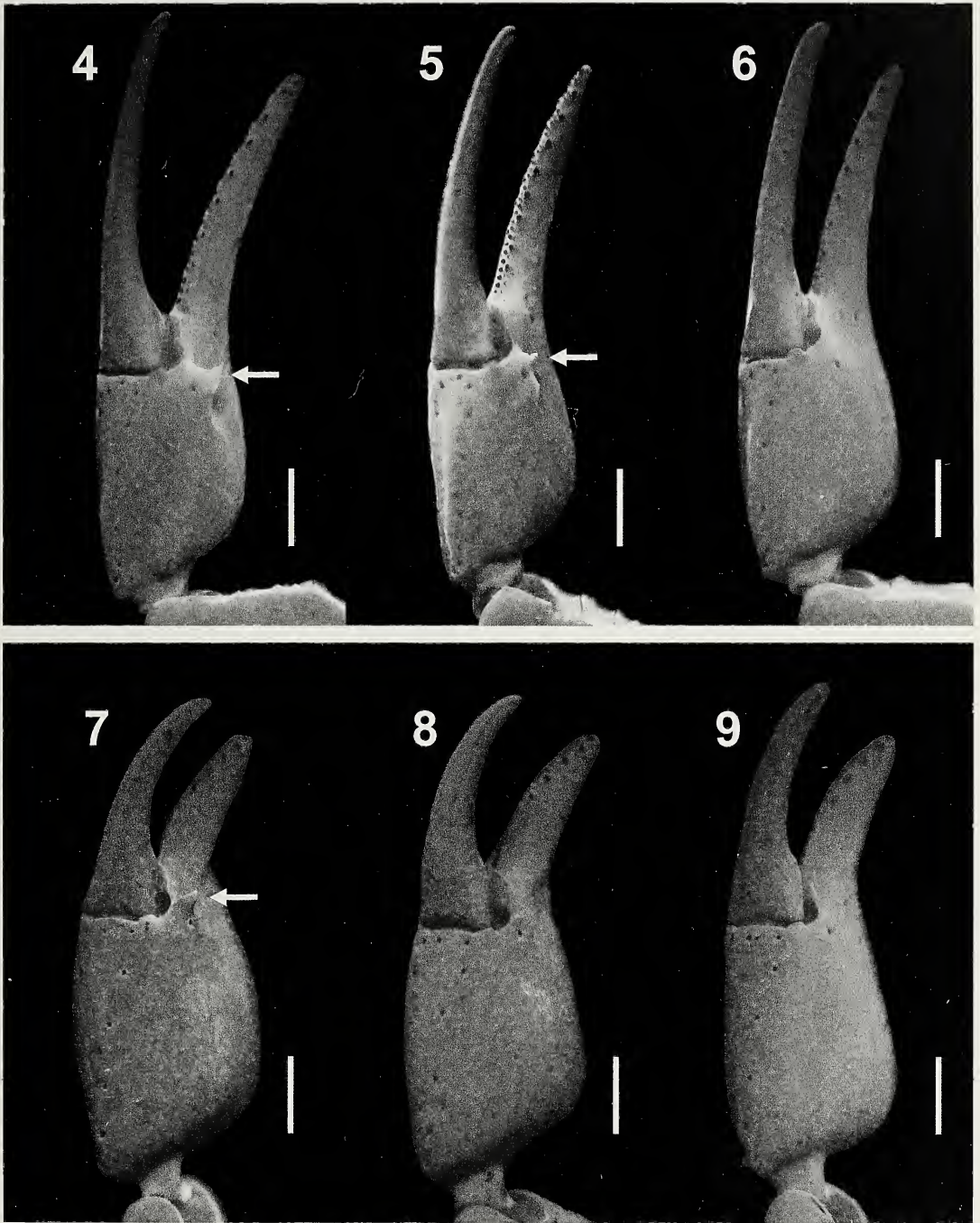
The pigmentation pattern of the malformed tergites is normal on the *Bothriurus coriaceus* and *B. noa* specimens, and apparently in the *Brachistosternus* (*L.*) *roigalsinai* female as well. However, in the latter case the specimen is not well fixed, and not all the pigmentation has been preserved.

Tergal malformations include division of tergites and fusion of tergal parts to one another. Armas (1976) described a fusion of tergite I to carapace, and Teruel (2004) observed division of tergites and fusion to metasomal segment I. All the specimens with anomalous tergites examined here were adult females. Teruel (2004) observed the same pattern but with four females and one male, and the specimen referred by Armas (1974) is an adult male. I have examined 226 specimens of *B. coriaceus* (57 females, 62 males and 107 juveniles), and found this kind of anomaly only on the two females referred to here (Mattoni 2003). Despite the few cases reported in scorpions, the presence of tergal malformations only on adults suggests that they arise during last molt.

The causes of these tergal malformations are completely unknown, but they do not seem to affect the life of the scorpion or its mating. The pigmentation pattern in the tergites of all the specimens appears not to be altered.

**Sexual malformations.**—*Brachistosternus* (*L.*) *pentheri*: The specimen has intermediate sexual characteristics: the small size and number of pectinal teeth (26/30, left/right) suggest that it is from a female, males possess larger and more numerous teeth (in the *B. pentheri* population from Ñacuñán the females usually have 25–32 teeth, and the males 32–41, Roig Alsina & Maury 1984); the telson is also more similar in shape to that of a female; the pedipalp chela has almost all the morphometric characteristics of a male, but the internal apophysis near the base of the movable finger (a sexual secondary structure present only on the males) is extremely reduced to approximately half of normal size (Figs. 4–6); the carapace surface is densely covered with blunt granules, as in regular males (females display fewer granules), but the tergites are smooth as





Figures 4–9.—Right pedipalp chelae, ventrointernal view. 4–6. *Brachistosternus pentheri*; 4. male; 5. intersexual specimen; 6. female. 7–9. *Bothriurus araguayae*; 7. male; 8. intersexual specimen; 9. female. Scale = 1 mm. The arrows show the secondary sexual structures.

in females (males display a fine granulation); sternites I–III present sparse granulation, and IV and V are smooth (on more typical males, all sternites are granular, whereas those of fe-

males are smooth); and the ventral surfaces of metasomal segments I to III are smooth as observed in females (these surfaces are granular on males). The specimen presents a paired

glandular surface on the dorsal side of metasomal segment V (another sexual secondary structure of males, Cekalovic 1973; Peretti 1997), but these glands are less well developed, being shorter than in regular males. The specimen also has well developed hemispermatophores, with sperm in the seminal duct, and testis tubules present; female genitalia (ovari-uterus, seminal receptacles and genital atrium) could not be found.

The presence of male, seemingly functional, sexual organs suggests that this specimen is an adult male with intersexual external morphology. Some of these characters are similar to those observed by Maury (1983) in a hermaphrodite *B. pentheri* male: poorly developed apophyses on the pedipalp chela, reduced dorsal glands on metasomal segment V, intermediate granulation on the carapace and tergites. The specimen described here presents more feminine external characters, like the pectines and telson, than those described by Maury (1983). The main difference between these specimens is the simultaneous presence of well developed embryos and hemispermatophores in Maury's specimen, which identifies it as a true hermaphrodite.

*Bothriurus araguayae*: The specimen exhibits many external characteristics of a female: smooth carapace and tergites (males typically present a fine and even granulation); absence of a sexual secondary gland on the dorsal side of the telson (present in adult males); metasomal segment V more robust than males, (which have slender segments, Lourenço & Maury 1979); and without an apophysis on the internal surface of the chela, behind the movable finger, that is present in the males, and is replaced in this specimen by a blunt granule (more pronounced than in regular females) (Figs. 7–9). The male characteristics of the specimen are as follows: both hemispermatophores present, pectines with larger and with more pectinal teeth, and genital operculum formed by two triangular isosceles plates (these are equilateral in females). I could not observe sperm in the seminal vesicles, because of the poor preservation of the reproductive organs. As in the previous case, I regard the *B. araguayae* specimen as a male, with intersexual external characteristics.

The main differences between the intersexual specimens of both species are related to secondary sexual structures: the internal

apophysis on the chela, which is absent in the *B. araguayae* specimen, and present, but reduced, in the *B. pentheri* specimen; and the metasomal glands, which are absent on the *B. araguayae*, and present, but reduced, in the *B. pentheri*.

These secondary sexual structures have a clear function during mating: the apophyses on the male chelae help to secure the female chelae during mating (Maury 1975; Peretti 1993), and the metasomal glands produce a secretion that reduces female resistance during mating (Peretti 1997). Further observations are necessary to understand the incidence of such developmental anomalies in scorpion populations, and the influence that they might have on life history (e.g., in reproductive biology), because of possible disadvantages of intersexual males in comparison with normal males.

The cause of these mutations among scorpions is unknown. Among other arthropods, intersexual specimens have been demonstrated to be the result of bacterial infection (Bouchon et al. 1998; Rigaud & Juchault 1998). We suspect that the intersexual phenomenon is not limited to the species described here but has been largely ignored in other species in which it may occur. Many external characters are widely used for determining the gender of scorpions, but only the dissection of a specimen can unequivocally confirm its sex, thereby allowing the identification of intersexual and hermaphrodite specimens. Also, one anomalous specimen can lead to a mistake, that was the case with the "male" of *Alayotityus juraguaensis* described by Armas (1984), a specimen with external female characteristics and with one paraxial organ, that led to Armas to say that this was the only species on the genus without sexual dimorphism. But in fact, as later discovered by Armas (1990), the specimen was a hermaphrodite, with one hemispermatophore and ovari-uterus.

I am indebted to Andrés Ojanguren-Affilastro for the information about the specimen of *B. noa*, to Glauco Machado for the donation of several specimens of *B. araguayae*, to Erich Volschenk for the help with the language, and to the curators of the collections from which material was loaned for study: Lorenzo Prendini (AMNH), Cristina Scioscia (MACN-Ar) and Luis Acosta (CDA). This note was



Table 1.—Reported cases and kind of anomalies in families of scorpions. The number of registered species showing the anomaly is in parentheses. The taxonomy presented in the table in accordance with Fet et al. (2000). However, see Stockwell (1989), Prendini (2000) and Sologlad & Fet (2003) for alternative hypotheses.

Anomaly	Family and species	Main references
Duplication of metasoma	Euscorpiidae (2) Buthidae (8)	Sissom & Shelley 1995 Vachon 1952; Sisson & Shelley 1995
Tergite division and/or fusion	Diplocentridae (3) Bothriuridae (3) Buthidae (1) Euscorpiidae (1)	Armas 1976; Teruel 2004 This work Teruel 2004 Teruel 2004
Leg malformation	Buthidae (4)	Armas 1977
Pedipalp chela compression on females	Bothriuridae (2) Buthidae (18) Chactidae (1) Chaerilidae (1) Diplocentridae (3) Euscorpiidae (3) Hemiscorpiidae (1) Liochelidae (1) Luridae (1) Scorpionidae (1)	Teruel 2004
Pedipalp fusion	Buthidae (1)	Cao & Solórzano 1991
Males with intersexual characters	Bothriuridae (2)	Maury 1983; this work
Males with one paraxial organ	Bothriuridae (1)	Peretti 2000
Hermaphrodite	Bothriuridae (1) Buthidae (2) Bothriuridae (1)	Maury 1983 Matthiesen 1968, Armas 1990 Maury 1983
Gynandromorphy	Buthidae (1) Diplocentridae (2)	Armas 1990 Cokendolpher & Sissom 1988

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## MODELING OF THE STRESS-STRAIN BEHAVIOR OF EGG SAC SILK OF THE SPIDER *ARANEUS DIADEMATUS*

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**ABSTRACT.** Spider silk has attracted the attention of many scientists because of its desirable physical properties. Most of this attention has been devoted to dragline silk, a thread that has high tensile strength, high strain and ultra-low weight. To help understand structure-property relationships in spider silks, the tensile behavior of egg sac (cylindrical gland) silk of *Araneus diadematus* Clerck 1757 was compared with dragline (major ampullate gland) and silkworm silks. In addition, stress-strain curves of egg sac silk were simulated by a spring-dashpot model, specifically a Standard Linear Solid (SLS) model. The SLS model consists of a spring in series with a dashpot and in parallel with another spring, resulting in three unknown parameters. The average stress-strain curve of fibers from five different egg sacs could be accurately described by the model. Closer examination of the individual stress-strain curves revealed that in each egg sac two populations of fibers could be distinguished based on the parameters of the SLS model. The stress-strain curves of the two populations clearly differed in their behavior beyond the yield point and were probably derived from two different layers within the egg sac. This indicates that silks in the two layers of *A. diadematus* egg sacs probably have different tensile behavior.

**Keywords:** Spider silk, tensile behavior, cocoon, cylindrical gland, tubuliform gland, Araneidae

Spider silk has attracted considerable attention as a natural fiber in the last 10 years because spider silk, especially dragline silk, shows a unique combination of high strength, high strain and extreme fineness. The silk produced by orb-web-weaving araneid spiders provides ideal material for studying the relationships between molecular structure and mechanical properties for protein-based structural materials. Araneid spiders have seven different gland-spinneret complexes, each of which synthesizes a unique blend of structural polymers and produces a fiber with a unique set of functional properties. An overview of the different spider silks of *Araneus diadematus* Clerck 1757, their glands, their function and amino-acid composition is provided in Table 1.

Spiders produce silks that range from Lycra-like elastic fibers to Kevlar-like superfibers, but it is not known how spiders modulate the mechanical properties of silks. Table 2 gives an overview of the tensile properties of spider silks and some other biological and engineering materials.

The spider silks that have been most studied are products of the major ampullate (MA) glands. The tensile strength (or a measure of the force needed to break a material) of MA silk is clearly higher than other polymeric biomaterials such as tendon collagen and bone as can be seen in Table 2. Moreover, because of its much higher strain to break value or extensibility, its toughness (as indicated by the work to rupture value in Table 2) or the energy required to break spider silk can be ten

Table 1.—Types and functions of spider silk for *Araneus diadematus* (Andersen 1970, Kaplan 1998). Small side chains for amino acids include glycine (Gly) + alanine (Ala) + serine (Ser)—polar = aspartic acid + threonine + serine + glutamic acid + tyrosine + lysine + histidine + arginine.

Silk	Gland	Function	Amino-Acids
Dragline	Major ampullate	Orb web frame, radii, dragline	Gly (37%), Ala (18%), small side chains (62%), polar (26%)
Viscid	Flagelliform	Prey capture, sticky spiral	Gly (44%), Pro (21%), small side chains (56%), polar (17%)
Glue-like	Aggregate	Prey capture, attachment to sticky spiral	Gly (14%), Pro (11%), polar glue (49%), small side chains (27%)
Minor	Minor ampullate	Orb web frame, bridging lines	Gly (43%), Ala (37%), small side chains (85%), polar (26%)
Egg sac	Cylindrical (tubuliform)	Reproduction	Ser (28%), Ala (24%), small side chains (61%), polar (50%)
Wrapping	Aciniform	Wrapping captured prey	Ser (15%), Gly (13%), Ala (11%), small side chains (40%), polar (47%)
Attachment	Piriform	Attachment to environmental substrates	Ser (15%), small side chains (32%), polar (58%)

times greater than that of other biological materials. Since initial modulus (for definition see Table 2) is a measure of stiffness, it is fair to say that spider MA silk is amongst the stiffest and strongest polymeric biomaterials known. However, the initial modulus or stiffness of MA silk is well below that of Kevlar, carbon fiber and high-tensile steel, engineering materials that are commonly employed to transmit and support tensile forces. Note also that the strength of MA silk is somewhat less than that of these engineering materials. Nevertheless, MA silk is still tougher than these engineering materials because of its large extensibility. See Table 2 for a summary of definitions concerning mechanical properties.

The viscid silk (Gosline et al. 1994) that forms the glue-covered catching spiral, is another truly remarkable spider silk material. Its initial modulus or stiffness is three orders of magnitude lower than that of MA silk and is comparable with that of a lightly cross-linked rubber. With a maximum strain of approximately 270%, viscid silk is not exceptionally stretchy compared to other rubbery materials, but its strength, at approximately 0.5 GPa, makes viscid silk roughly ten times stronger than any other natural or synthetic rubber.

Of all the silks, MA silk has been an object of desire for materials engineers because of its extreme performance properties, particularly its strength. Investigators have already been searching for more than 15 years to pro-

duce "synthetic" dragline silk in quantities sufficient for applications such as bullet-proof vests, parachute cords, surgical sutures and substitutes for ligaments. However, commercial production of "synthetic" MA silk is still not possible. We have focused on the mechanical and structural properties of spider silk of the egg sac, which to this point, is not well studied. We believe that it is precisely through correlating chemical, microstructural and consequent property differences between silks that knowledge of how the spider controls the fiber function will be acquired.

Egg sac silk is secreted by the cylindrical (= tubuliform) glands. At any point along its length, the egg sac fiber must be able to bend easily in one plane but otherwise resist bending and stretching. As reported by Barghout et al. (2001), these mechanical properties are imparted by a multiaxial anisotropic microstructure that is not observed for MA silk. Barghout et al. (1999) also observed the presence of non-periodic lattice crystals identified previously in the MA silk of *Nephila clavipes* Linnaeus 1767 (Thiel et al. 1997). Moreover, they found that these crystals in *A. diadematus* Clerck 1757 egg sac silk are twisted parallel to the chain direction in contrast to what is found for MA silk. This is suggested to be the reason for the lower stiffness that is found for *A. diadematus* egg sac silk compared to MA silk (Stauffer et al. 1994).

Stauffer et al. (1994) compared the physical



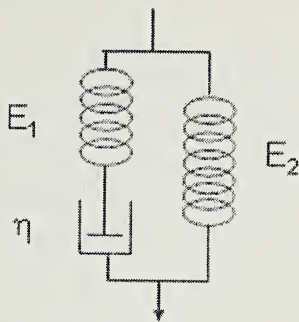


Figure 1.—The standard linear solid model that was used to simulate the stress-strain behavior of egg sac silk of *Araneus diadematus*.

properties of three silks (secreted by the major ampullate, minor ampullate and cylindrical glands) from *N. clavipes* and *Araneus gemmoides* Chamberlin & Ivie 1935. Comparing silks within each species, they concluded that major ampullate silk is substantially stronger than either of the other two silks. Egg sac silk is next, followed closely by minor ampullate silk. The strain of these different silks seemed comparable.

The dominant, repeated crystallizable motifs in egg sac silk of *A. diadematus* are similar to the motifs that form  $\beta$ -sheet crystals in MA silk spun by *N. clavipes* (Guerette et al. 1996; Thiel et al. 1997). The number of times these motifs are repeated for *Araneus* egg sac

silk are however somewhat smaller than the corresponding values for *Nephila* MA silk. From the materials science viewpoint it is expected that similar primary structures at the molecular level will lead to similar ordering schemes at microstructural scales. This viewpoint is axiomatic in our use of egg sac silk to obtain further insights into the structure of MA silk. Working with *Araneus* egg sac silk offers a significant advantage relative to working with MA silk: useful amounts are produced in a convenient (compact) form.

In a previous study (Van Nimmen et al. 2003), the effects of UV-light and humidity on the stress-strain properties of egg sac silk of *A. diadematus* were demonstrated. Another study (Van Nimmen et al. 2004) considered the effect of strain-rate on the tensile properties of egg sac silk of *A. diadematus*.

The aim of the present study was to investigate how the stress-strain behavior of egg sac silk compared with the behavior of drag-line silk and cocoon silk obtained from silkworms. We expected that spider egg sac and silkworm cocoon silks would have similar tensile properties because they serve similar functions (providing shelter and protection). Attention was focused on the shape of the stress-strain curves.

Mechanical properties are often characterized only by breaking force, breaking strain

Table 2.—Tensile mechanical properties of spider silks and other materials as derived from the literature (Gosline et al. 1999; Denny 1976). Initial modulus is defined as the modulus in the elastic range of the diagram in which strain changes are still reversible, it is usually calculated from the slope of the initial elastic region of the force-strain curve, also the term stiffness is used; strength (or tensile strength) is a measure for the breaking force or the force required to break the material; strain to break is the increase in length of a specimen produced by the breaking force, usually expressed as a percentage of the original length; toughness is a measure of the required energy to break a material and is calculated as the area contained by the force-strain curve up to the breaking point, often indicated as the work to rupturevalue.

Material	Initial modulus (GPa)	Strength (GPa)	Strain to break (%)	Work to rupture (MJ m <sup>-3</sup> )
<i>Araneus</i> MA silk	10	1.1	27	160
<i>Araneus</i> viscid silk	0.003	0.5	270	150
<i>Bombyx mori</i> silk	7	0.6	18	70
Tendon collagen	1.5	0.15	12	7.5
Bone	20	0.16	3	4
Elastin	0.001	0.002	150	2
Resilin	0.002	0.003	190	4
Synthetic rubber	0.001	0.05	850	100
Kevlar 49	130	3.6	2.7	50
Carbon	300	4	1.3	25
High-tensile steel	200	1.5	0.8	6

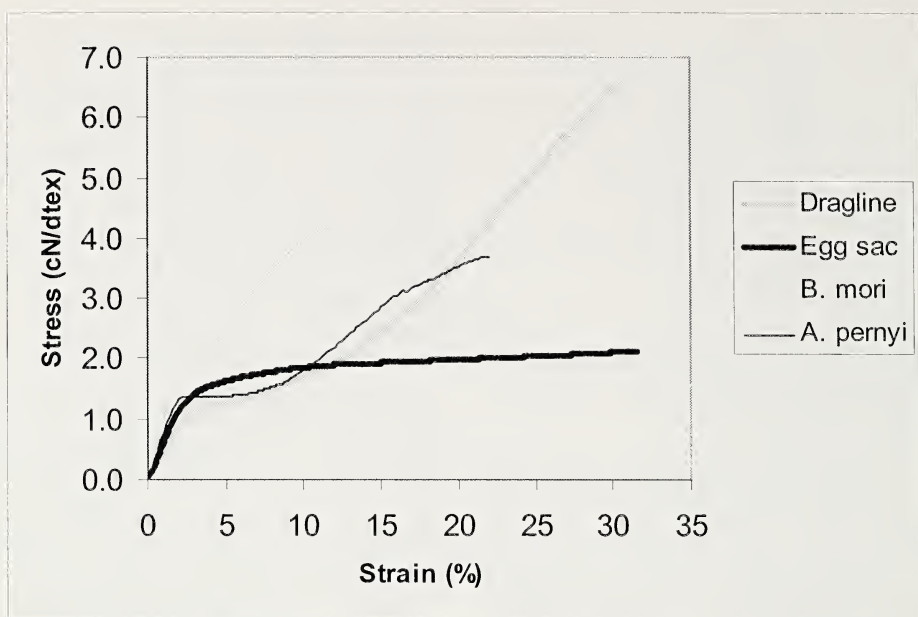


Figure 2.—The average stress-strain curves of different silks as measured by a single-strength tester (gauge length 20 mm, testing speed 20 mm/min) based on 169 tests of *Araneus diadematus* dragline silk, 403 tests of *A. diadematus* egg sac silk, and 49 tests each of *Bombyx mori* and *Antheraea pernyi* silk.

and initial modulus. However, we are also interested in the time-dependent behavior that is also partly included in the stress-strain curves. In this study, visco-elastic models, based on spring-dashpots, are used to simulate the stress-strain behavior for spider egg sac silk. This will help to relate the mechanical and visco-elastic characteristics to the structural properties that will be investigated in further research. Finally, because of the high variability that was noted for the tensile properties within each egg sac, a cluster analysis was performed in order to find out if different fiber populations or layers could exist within an egg sac.

## METHODS

**General methods.**—Five egg sacs of *Araneus diadematus* Clerck 1757 were collected in a bower in Belgium (Merelbeke, 51° north latitude and 3° east longitude) in autumn. One of these *A. diadematus* spiders with her egg sac is deposited as a voucher specimen in the “Zoology Museum” (UGMD 104091), Ghent University in Belgium.

Since the egg sacs were collected in their natural habitat, we expected that the measured mechanical behavior would better represent the real characteristics than if they were produced by lab-reared spiders. The egg sacs

were removed shortly after oviposition. After removing the clearly visible outer cover, one hundred fibers were gently removed at random from the inside of each egg sac, with care taken to stress the fibers as little as possible.

For the dragline samples, some *A. diadematus* were reared in the laboratory and from thirty spiders a sample of dragline thread was manually reeled off as spiders hung freely suspended in space. From every sample, ten fibers were prepared and tested.

Fibers were also tested from cocoons of the silkworms *Bombyx mori* and *Antheraea pernyi* (Tussah silk), grown at the Silk Museum of Meliskerke (The Netherlands). Since the samples we obtained were already a thorough blend of fibers of different cocoons, we decided to reduce the number of tests to 50 for both silks. All samples were kept in a conditioned laboratory of  $20\text{ }^{\circ}\text{C} \pm 2\text{ }^{\circ}\text{C}$  and relative humidity of  $65 \pm 2\%$  for at least 24 hours before testing.

The FAVIMAT-ROBOT (Textechno) was used to analyze the tensile properties of the egg sac, cocoon and dragline fibers. It is a semi-automatic single fiber strength tester, working according to the principle of constant rate of extension (standards: DIN 51221, DIN 53816, ISO 5079). The instrument is equipped



with a balance allowing the mass to be measured at a high resolution of 0.1 mg. Moreover, this instrument includes an integrated measuring unit for linear density i.e.; mass per unit length, expressed in dtex, which equals decigrams per kilometer. This measure has the considerable advantage that the linear density, a measure for fineness, is determined simultaneously with the tensile properties. This is particularly advantageous for natural fibers. The linear density is measured according to the vibroscopic method (ASTM D 1577-BIS-FA 1985/1989 chapter F).

Because of the extreme fineness of dragline thread, it was unfortunately not possible to simultaneously determine the linear density of the dragline fibers. Instead, diameters of these fibers (in  $\mu\text{m}$ ) were measured on a large number of samples with image analysis on a light microscope and the conversion was made to dtex taking into account a specific density of  $1.3 \text{ g/cm}^3$  as reported in the literature (Vollrath & Knight 2001).

The tensile properties were tested in standardized conditions of  $20 \pm 2^\circ\text{C}$  and relative humidity of  $65 \pm 2\%$  with a gauge length of 20 mm, a test speed of 20 mm/min, and a pre-tension of 0.05 cN/dtex. For the linear density, a test speed of 5 mm/min and a pre-tension of 0.08 cN/dtex were applied.

**Visco-elastic models.**—*The Maxwell model:* The stress-strain curve of polymers is often mathematically described by models indicating the visco-elastic behavior of these polymers. When a material is extended by an applied force, there is, besides the elastic component, a further component whose action opposes the applied force but whose magnitude depends on the speed of extension. This second component decays relatively slowly with time. When the applied force is subsequently removed, the same component also acts to resist the internal elastic forces that bring about contraction. This time dependency of polymers is also indicated as visco-elasticity (Saville 1999). Their behavior is fitted by a visco-elastic model as the relationship between the applied stress and resultant strain contains a time-dependent element.

Most visco-elastic models consist of a combination of springs and dashpots. The spring represents the elastic solid-like behavior where Hooke's law is valid ( $F = E\varepsilon$  where  $F$  is load or force,  $E$  is elastic modulus and  $\varepsilon$  is strain), whereas the dashpot represents the

time-dependent, viscous liquid-like behavior where Newton's law is valid ( $F = \eta(d\varepsilon/dt)$  where  $\eta$  is the viscosity or damping constant).

In the simplest Maxwell-model (Tobolsky et al. 1951), the visco-elastic behavior of a fiber (or yarn) is described by a spring (with elastic modulus  $E$ ) and a dashpot (with damping constant or viscosity  $\eta$ ) in series. This behavior obeys the following equation (with the strain and  $F$  the force):

$$\frac{d\varepsilon}{dt} = \frac{1}{E} \frac{dF}{dt} + \frac{F}{\eta} \quad (1)$$

This model is often used to describe stress-relaxation, a phenomenon that is observed when a polymer is extended by a given amount and then held at that extended length. If the force required to do this is monitored, it is found to rise immediately to a maximum value and then slowly decrease with time.

To use this model to describe stress-strain curves in tensile testing, we take into account a constant increase of strain with time, so that we can pose that  $\varepsilon = r t$ , with  $r$  a constant.

Equation (1) then becomes:

$$r = \frac{1}{E} \frac{dF}{dt} + \frac{F}{\eta} \quad (2)$$

with as starting condition  $F(0) = F_v$ , where  $F_v$  is the preload, from which the following solution is obtained:

$$F(\varepsilon) = F_v + \eta r \left[ 1 - \exp\left(-\frac{E}{\eta r} \varepsilon\right) \right] \quad (3)$$

Equation (3) can be written as:

$$F(\varepsilon) = F_v + A(1 - e^{-B\varepsilon}) \quad \text{with} \\ A = \eta r \quad \text{and} \quad B = \frac{E}{\eta r} \quad (4)$$

This equation allows parameters  $A$  and  $B$  to be estimated by means of a non-linear regression.

**The standard linear solid model:** An extension of this Maxwell model is the so-called standard linear solid (SLS) model, where a linear spring in parallel is added (Fig. 1).

Taking into account this spring in equation (2) and by differentiating, equation (4) can then be written as follows:

$$F(\varepsilon) = F_v + A(1 - e^{-B\varepsilon}) + C \cdot \varepsilon \quad \text{with} \\ A = \eta r \quad \text{and} \quad B = \frac{E}{\eta r} \quad \text{and} \quad C = E_2 \quad (5)$$

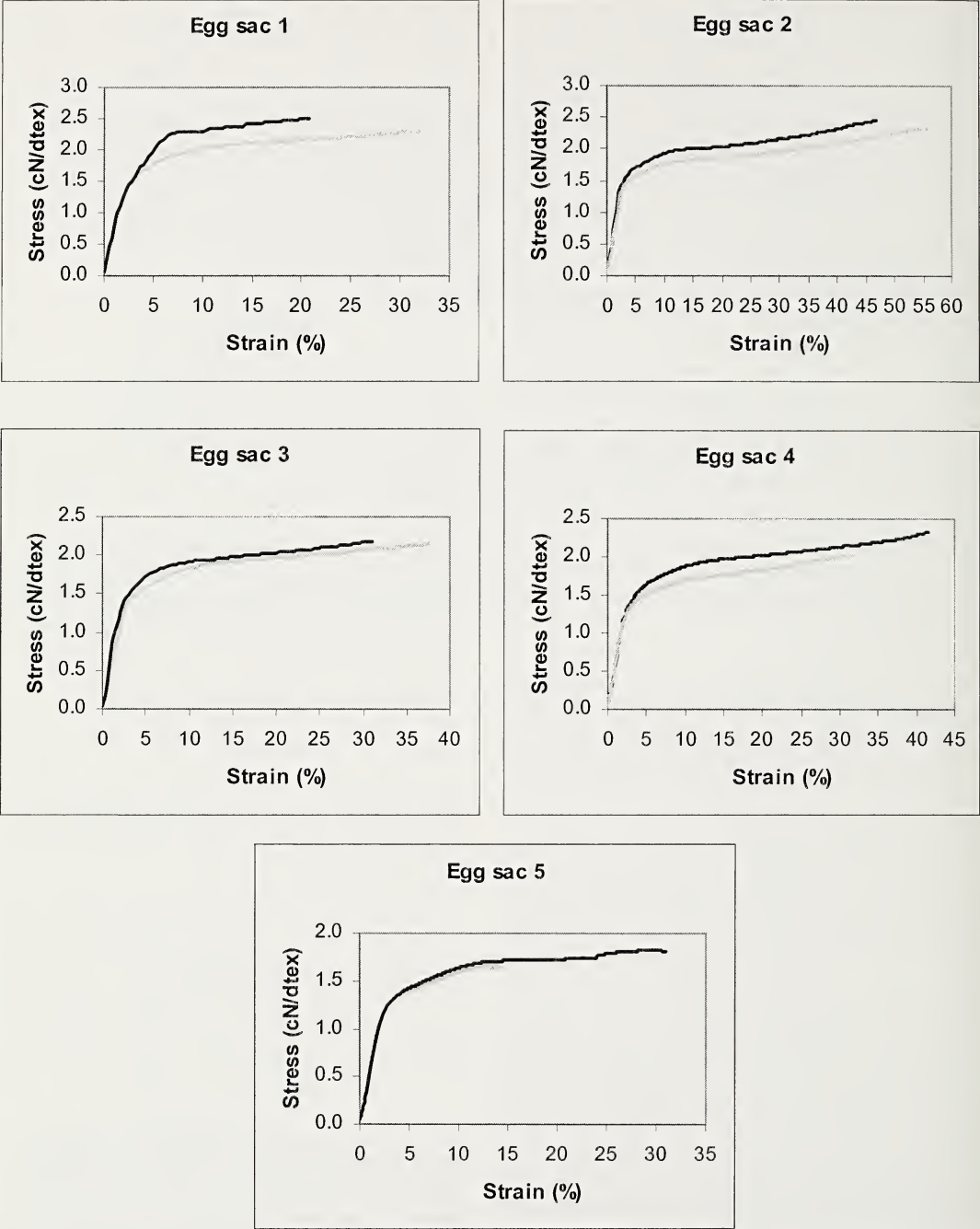


Figure 3.—Simulation by means of the standard linear solid model for two statistically different fiber populations found within an egg sac by means of a cluster analysis.

The parameters A, B and C can then be estimated by means of non-linear regression.

*The Voigt model:* Another time-dependent phenomenon is creep. If instead of a fixed extension, a fixed force is applied to the mate-

rial, an initial extension of a magnitude is found that is expected from the force-strain curve followed by a further slow extension with time. For the description of creep or tensile testing under constant increase of load,



Table 3.—The average values (Mean) and the standard deviations (SD) of the parameters A, B and C of the SLS model for the 5 egg sacs of *Araneus diadematus* for 2 statistically different fiber populations ("1" and "2") as found by means of a cluster analysis ( $n$  = number of fibers within each population).

	A		B		C		<i>n</i>
	Mean	SD	Mean	SD	Mean	SD	
Egg sac 1							
1	1.84	0.14	0.46	0.05	0.015	0.010	52
2	2.39	0.20	0.36	0.06	−0.006	0.021	14
Combined	1.95	0.28	0.44	0.06	0.010	0.015	66
Egg sac 2							
1	1.75	0.05	0.50	0.05	0.013	0.003	33
2	1.58	0.04	0.51	0.07	0.012	0.001	27
Combined	1.67	0.09	0.50	0.06	0.012	0.002	60
Egg sac 3							
1	1.70	0.07	0.42	0.04	0.011	0.002	31
2	1.72	0.15	0.54	0.03	0.012	0.003	24
Combined	1.71	0.11	0.47	0.07	0.011	0.003	55
Egg sac 4							
1	1.72	0.11	0.45	0.07	0.013	0.002	43
2	1.48	0.11	0.56	0.09	0.016	0.004	29
Combined	1.62	0.16	0.50	0.10	0.014	0.004	72
Egg sac 5							
1	1.28	0.11	0.58	0.06	0.021	0.007	19
2	1.50	0.13	0.47	0.05	0.010	0.003	48
Combined	1.44	0.16	0.50	0.07	0.013	0.007	67

the simplest model used is the Voigt model. This model consists of a spring (elastic constant  $E$ ) in parallel with a dashpot (with damping constant  $\eta$ ). The visco-elastic behavior is then described by the following differential equation (with  $\varepsilon$  the strain and  $F$  the force):

$$F = E\varepsilon + \eta \frac{d\varepsilon}{dt} \quad (6)$$

Using the correct starting conditions for creep or tensile testing under constant increase of load, solutions for this equation can be found. Since these are not valuable for this study, the reader is referred to the literature (Saville 1999).

**Other visco-elastic models:** The models described above can be extended to more elements, such as the "four-elements model" consisting of a Maxwell-element in series with a Voigt element or more generalized Maxwell and Voigt models considering a finite or infinite number of Maxwell or Voigt elements connected in parallel or in series. Since it is beyond the scope of this study, the

reader is again referred to the literature for further description (Saville 1999).

## RESULTS

**The tensile behavior of silks.**—First, it should be remarked that although 500 egg sac fibers and 300 dragline fibers were tested, not all were successful mostly due to the fineness of the fiber. For the calculation of the average stress-strain curves, for which the shape is the most important, only curves with strain to break values higher than 10% were considered. The curves were stopped at the average strain to break values of all available tests. It can be expected that the measurements show a small error since probably the weakest fibers could not be tested. However, from the histogram of the strength values, the contribution of stronger fibers is not higher than that of the weaker fibers. In addition, the high variability in the stress-strain curves among the different egg sacs should be noted, which can also be found in the literature on dragline silks (Madsen et al. 1999; Garrido et al. 2002).

Fig. 2 shows the average stress-strain curves of the different silks of *A. diadematus* (dragline, egg sac), *B. mori* and *A. pernyi*. It is clear that egg sac silk shows a completely different stress-strain behavior from dragline silk and even the functionally comparable silkworm cocoon silks. All stress-strain curves start with a small elastic region. For the dragline, *B. mori* and *A. pernyi* fibers, this region is followed by a plastic region and finally by strain hardening where the stress again linearly increases with strain. However spider egg sac silk shows a plastic-hardening region that is extremely flat. Since in this region the stress increases again linearly with strain, we will simply use the term "hardening region" to indicate this region.

Although egg sac silk shows about the same strain to break as dragline silk, the tensile strength of dragline silk is three to four times higher. The initial modulus (calculated from the slope of the initial straight line portion), which is a measure of stiffness of the fiber, is significantly higher for egg sac silk than for dragline thread (67 cN/dtex versus  $\pm 47$  cN/dtex) ( $P < 0.001$ ).

**Simulation of tensile behavior of egg sac silk.**—For this research, the stress-strain data of the five egg sacs were used, from which the average stress-strain curve shown in Fig. 2 was produced. Since we were working with tensile testing with constant increase of extension, the Maxwell-model as described earlier was used to describe the stress-strain behavior. Starting from equation (4), the parameters A and B were estimated by means of a non-linear regression. We concluded that the Maxwell-model does not completely satisfy the simulation of the stress-strain curve for the egg sac silk fibers.

We then applied the SLS model, in which the 3 parameters A, B and C of equation (5) were estimated by means of a non-linear regression. With the average data of the stress-strain curves, for each egg sac a correlation of higher than 99% with a relative error (defined as  $(F_{\text{experimental}} - F_{\text{predicted}})/F_{\text{experimental}}$ ) smaller than 0.1% was observed, except in the initial elastic region where the maximum relative error at about 0.4–0.5% strain exceeds 0.4% to 1%.

To get an indication of the variability within the egg sac, the non-linear regression was repeated for each of the individual stress-strain

curves of the 100 fibers that were tested for each of the five egg sacs. Because of the observed high variability, we performed a cluster analysis (with the statistical software SPSS) on the estimated parameters A, B and C in order to identify statistically different clusters or fiber populations.

The result of this cluster analysis is given in Table 3. Within the different egg sacs, two clusters (indicated as "1" and "2") of statistically different fiber populations could be detected. In this analysis, clusters of less than 10 fiber data were removed. The clusters or fiber populations for egg sac 1, egg sac 4 and egg sac 5 show completely different A, B and C values. In other words, the level of the more horizontal hardening region (indicated by A), the shape of the yield (or transition) region (indicated by B) and the slope of the hardening region (indicated by C) of their stress-strain curves are significantly different. For egg sac 2, only the A-values of the clusters are significantly different, while the confidence regions of the parameters B and C are overlapping. With respect to egg sac 3, the B-values of the clusters are significantly different, while the confidence regions of the parameters A and C are overlapping.

Based on the cluster analysis, the stress-strain curves of the individual fibers from each egg sac were split into 2 groups and the average curve of each group was calculated. These average stress-strain curves based on the two different fiber populations for each egg sac are shown in Fig. 3. It can be concluded that the fiber populations seem to differ mostly in the level of the relatively flat so-called hardening region and thus the breaking stress value. The initial modulus and the modulus of the hardening region, i.e. the tangent modulus at the yield point, seem to be quite equal for both fiber populations.

## DISCUSSION

**The tensile behavior of silks.**—The shapes of the stress-strain curves that we found and that were also seen by Van Nimmen et al. (2004) are similar to those that were found by Stauffer et al. (1994). However, Stauffer et al. 1994 determined different absolute values for strength and strain. As their testing procedures were different from our, it is difficult to evaluate the discrepancies. They found for *Ara-neus gemmoides* MA silk final breaking points



at extensions of about  $15 \pm 2\%$  ( $n = 10$ ) with a final stress of  $4.7 \pm 0.5$  GPa and for egg sac silk breaking strains at  $19 \pm 2\%$  ( $n = 10$ ) with tensile strengths of  $2.3 \pm 0.2$  GPa. They obtained much higher stress values than found elsewhere for MA silk (see Table 2) because, for diameter measurements, they took into account the ten smallest diameter points in several sections of the silks. With respect to strain, we found much higher values ( $30 \pm 9\%$ ,  $n = 183$ ) for MA silk and  $32\% \pm 16\%$ ,  $n = 398$  for egg sac silk), with a much higher variability, probably due to the greater number of tests performed. It is not clear if this difference is due to the difference in testing procedure or to the spider species. However, other published data of MA *Araneus* silk mention a strain to break value of 27% (Denny 1976) which agrees better with our strain data. In order to make further comparisons possible with the tensile properties presented in Table 2, our breaking stress and stiffness values were converted to the GPa unit, taking into account a specific density of  $1.3 \text{ g/cm}^3$  (Vollrath & Knight 2001). The breaking stress values thus obtained were  $0.94 \pm 0.36$  GPa ( $n = 183$ ) for MA silk and  $0.27 \pm 0.05$  GPa ( $n = 398$ ) for egg sac silk.

The stiffness values, calculated from the slope of the initial elastic region, resulted in values for MA silk of  $6.1 \pm 2.4$  GPa ( $n = 167$ ) and for egg sac silk of  $8.7 \pm 0.9$  GPa ( $n = 434$ ). The stiffness value for MA silk seems low compared to the value of 10 GPa that is given in Table 2. Probably the testing conditions play a role in this difference (forced or unforced silking, single or multifilament, climate, strain rate, gauge length, etc.). Denny's (1976) analysis of the strain-rate dependence of MA silk demonstrated that the initial stiffness increases from 9.8–20.5 GPa when the strain rate is increased from  $0.0005 \text{ s}^{-1}$  to  $0.024 \text{ s}^{-1}$ . Also the spinning conditions (e.g. drawing speed, body temperature) have been reported to affect the tensile properties (Vollrath et al. 2001).

We believe the different stress-strain behavior of dragline and egg sac silk is partly due to different amino acid compositions. Glycine (Gly) and alanine (Ala) are most abundant in draglines, while serine (Ser) and Ala are most abundant in egg sac silk (Table 1). Moreover, the proline rich motif Gly-Pro-Gly-X-X occurs in dragline silk but not in egg sac silk

(Guerette et al. 1996; Gosline et al. 1999). Thiel et al. (1997) believe that the structure of the proline residue forces a severe kink in an extended backbone chain. On the other hand, the total content of the small amino acids Gly, Ala and Ser, which is usually taken as an indication of crystal forming potential (Gosline et al. 1986), is almost the same for dragline and egg sac silk (Table 1). Thus, we would expect the crystallinity of both fibers to be similar. However, in tensile testing, the weakest regions, i.e. the more amorphous regions, most affect the stress-strain behavior. Consequently, two silks with similar crystallinity may exhibit dissimilar tensile properties. Thus, the different stress-strain curves of MA and egg sac silk are probably more a reflection of differences in the arrangement (chain lengths, number of coils, etc.) of the structural elements of the amorphous regions than of the crystalline domains.

Since glycine is the simplest amino-acid (side group H), while serine is an amino-acid with a much more voluminous side group ( $\text{CH}_2\text{OH}$ ), the difference in strength between dragline and egg sac silks may be mainly attributed to the more compact structure which can be built with glycine, resulting in a structure that is more resistant to stress. Although the structure of the glycine-rich regions of MA silk is imperfectly understood, there is consensus that these regions are part of a more oriented amorphous phase (Jelinski et al. 1999; van Beek et al. 2002). Moreover, the proline-rich regions in MA silk are expected to include more turns, resulting in a higher number of hydrogen bonds and thus in a more stress resistant structure. A more intensive study of the spinning process, structure and morphology of spider silk, especially egg sac silk, is required to further explain the difference in tensile behavior.

We also note that the shapes of the stress-strain curves obtained for the silkworm silks are more similar to dragline silk than to egg sac silk, even though the silkworm and spider use the former two silks for completely different functions. Since the main constituents of *B. mori* and *A. pernyi* silks are also glycine and alanine (44% Gly, 29% Ala, 12% Ser in *B. mori* and 27% Gly, 43% Ala, 11% Ser in *A. pernyi* (Kishore et al. 2002)), the higher similarity in behavior to dragline silk could be expected.

**Simulation of tensile behavior of egg sac silk.**—The different fiber populations vary mostly in the hardening region, that is, the region beyond the yield point. The initial elastic region, and the modulus of this region, that is usually used to define the stiffness, appears not to differ for the two fiber populations. As mentioned before, the spring in the SLS model represents the solid character whereas the dashpot indicates the liquid character. By adding a (elastic) spring to the Maxwell model, an element is added that results in a linear relation between stress and strain beyond the yield point. The significance of the coefficient C indicates that there is indeed a significant, although small, increase in stress as a function of strain beyond the yield point. During post-yield extension, the long molecules tend to become oriented along the stress axis and, as a result, a structure may be obtained which approaches that of a crystalline material. This is, in fact called "strain-induced crystallization" (Wainwright et al. 1976) and leads to a notable increase in the value of the instantaneous elastic modulus. A link with the twisted non-periodic lattice (NPL) crystals demonstrated by Barghout et al. (1999) can be made. The twist of these regions may result in the flattened behavior beyond the yield point, i.e. the lower tangent modulus at the yield point, for egg sac silk compared to dragline silk (in which the twist of the NPL crystals is not observed).

Since the fibers were randomly selected from each egg sac, the two fiber populations can probably be attributed to different layers that constitute the egg sac. Our own preliminary structural research of the egg sac of *Araneus diadematus* indeed confirms the existence of different layers, especially observed as a slight difference in color and in the stacking of the fibres above and below the eggs. Different layers in the egg sac structure are also found for the spider *Zygiella x-notata* (Gheysens et al. in press). A more detailed study in which an attempt is made to divide the different layers will be required to confirm this.

This study has shown that egg sac silk of *Araneus diadematus* has a completely different tensile behavior from dragline of the same spider. In contrast to what was expected given the functions of the different silks, more similarities were found between spider dragline

silk and cocoon silks of *Bombyx mori* and *Antheraea pernyi* than between the latter and the spider egg sac silk. We suggest that the difference in stress-strain behavior is partly due to the different amino acid composition, and especially the structure of the amorphous domains. A further structural and morphological study of egg sac silk is required to further explain its special stress-strain behavior.

The stress-strain curve of spider egg sac silk can be accurately simulated by the standard linear solid model with 3 parameters to be estimated. A more detailed analysis of the estimated parameters A, B and C revealed that for each egg sac two clusters or populations of fibers could be found, mostly differing in the stress level of the region beyond the yield point. Since the fibers were taken randomly from each egg sac, it is suggested that the different behavior of the two fiber populations is due to the different tensile behavior of two layers constituting an egg sac. A further study will be required to relate the mechanical properties to the functions of these different layers.

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Figures 27–34.—Right chelicerae of species of *A-us* from Timbuktu: 27, 29, 31, 33. Dorsal views; 28, 30, 32, 34. Prolateral views of moveable finger; 27, 28. *A-us x-us*, holotype male; 33, 34. *A-us y-us*, male. Scale = 1.0 mm.

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Short Communications are usually limited in length to three journal pages, including tables and figures. They will be printed in a smaller (10 point) typeface. The format for these is less constrained than for feature articles: the text must still have a logical flow, but formal headings are omitted and other deviations from standard article format can be permitted when warranted by the material being covered.



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